

AN ANALYSIS OF VOCALIZATIONS
OF THREE SPECIES OF EAST AFRICAN CERCOPITHECIDAE

By

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With Love
to
Mom, Dad, and Bruce

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Abstract of Dissertation Presented to the Graduate Council
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AN ANALYSIS OF VOCALIZATIONS
OF THREE SPECIES OF EAST AFRICAN CERCOPITHECIDAE

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Vocalizations of three species of Old World monkeys (Sykes monkey, Cercopithecus mitis; colobus monkey, Colobus polykomos; and baboon, Papio cynocephalus) were collected in Kenya, East Africa. Sonograms of the vocalizations were made and analyzed in terms of their physical characteristics (frequency, duration, and tonality). Representative sonograms are illustrated and tables of all measurements made are presented. Accompanying behavioral information is also included whenever available.

Fourteen Sykes vocalizations are catalogued and described. An analysis of the calls in terms of discreteness and gradedness revealed that most of the vocalizations were of the discrete type.

The Sykes vocalizations were also examined to see if physical properties, or structure, could be related to function. It was found that those calls transmitted over distances which were important for group cohesion and alarm or

threat were structured so as to facilitate locating the caller. Calls operating at close-range did not have such localizing properties.

The question of whether Cercopithecus mitis is conspecific with C. nictitans has been raised in the literature. This study evaluated the taxonomic status of these two species. Based on similarities and differences in the vocalizations it was concluded that separate specific identity should be maintained. However, C. mitis was found to be more closely related to C. nictitans and C. erythrotis-cephalus than to the mona superspecies.

Five vocalizations of the colobus monkey are described: two for infants, one for juveniles, and two for adults. A nonvocal behavior pattern, the jumping display, was found to be of communicative significance in alerting a troop to danger and in indicating the direction of troop movement. It also functioned as an intimidation display directed at the observer.

The role which vocalizations play in the crop-raiding activities of baboons was investigated and the apparent "decoy" effect of the calls in distracting the attention of Africans protecting the fields was examined. It was concluded that the vocalizations did not represent a deliberate and planned decoy tactic, but instead were a fortuitously diversionary behavior which contributed incidentally to the success of the raids. Four types of calls given during the raids are described.

CHAPTER I

INTRODUCTION

The study of primate communication is assuming an increasingly important role in the field of primatology. As more is learned of the behavior of man's closest relatives, the nonhuman primates, the more apparent it has become that understanding how behavior patterns are transmitted and interpreted will contribute considerably to understanding the adaptive mechanisms of social life. Many of the earlier studies on primate behavior, and even some of the more recent, either failed to include communication as an aspect of behavior to be investigated or else dealt with it in such a cursory and unscientific manner as to make it almost worthless for further investigation and comparison. Part of the problem is no doubt related to the all-pervasive nature of communication into all aspects of social life, a fact which is well illustrated by the following definition: "...social communication is the process by which the behavior of an individual affects the behavior of others" (Altmann, 1967:326).

Communication as it has been defined can include many different forms of behavior occurring in concert and involving several individuals. It becomes apparent, therefore, that the study of communication can be a complex undertaking.

Further complications become apparent when one considers that communication can take place via several different channels. Signals or messages may be olfactory, tactile, visual, or auditory in nature and for any specific signal transmission several of these channels of communication may be used simultaneously. Each of these channels has been investigated in studies of communication among the primates (see Andrew, 1963a, 1964; Bolwig, 1964; Hinde and Rowell, 1962; Jolly, 1966; Moynihan, 1967; van Hooff, 1962).

The Study of Primate Vocalizations

The primary concern of the present study, however, will be with primate vocal communication, the study of which has taken various forms.

One approach consisted of transcribing the various calls by using letters of the alphabet in order to give as close an approximation as possible of the sound of the call (for an example see Ullrich, 1961). Not only was this system largely subjective in nature, but the alphabetical notation used was generally that of the language of the observer and hence was not accessible to, or reproducible by, researchers of all nationalities. In order to overcome some of the subjectivity of such an approach and to insure a certain amount of uniformity, there was an attempt to use the standard International Phonetic Alphabet (for an example see Hill and Booth, 1957). However, it soon became apparent that non-human primates were capable of producing sounds which

lacked counterparts in human speech. Phonetic and alphabetical transcriptions, therefore, could not render an accurate description of many vocalizations and often gave a false, human quality to the vocal patterns of primates other than man.

The most common approach to the study of primate vocal communication until recently has been the assignment of a descriptive name to a vocalization, one which depicts as closely as possible the type of call given. In this way such terms as 'squeal', 'click', and 'grunt' were used but were really only of value when as complete an acoustic description as possible accompanied the assignment of such a term. Moreover, adjectives such as 'high-pitched', 'shrill', 'harsh', etc., used in such descriptions, were still ambiguous and subjective in nature. Hence, comparisons of vocalizations reported in different studies remained difficult, if not impossible, to carry out.

The problem of subjectivity was alleviated to a considerable extent with the development within the last two decades of sophisticated, sensitive recording devices and the invention of the sound spectrograph. The spectrogram, or sonogram, supplies a permanent, visual record of a sound and serves both as a form of notation and as a method of precise measurement. Although descriptive terms remain prevalent as names or labels for the various calls, they are now supported by a more concrete, objective, physical description than was possible before.

Receiving its impetus largely from studies on insects, anurans, and birds, the use of sonograms in the study of primate vocalizations has spread rapidly within the last several years. Most of the work on primate communication has been with species of Old World monkeys, especially the macaques, baboons, and vervets. Rowell (1962) used sonograms and described nine agonistic noises of the rhesus macaque, relating each to the various postures and expressions which they accompany. Struhsaker (1967) has done an excellent spectrographic analysis of vervet vocalizations combining a detailed physical description of the calls with behavioral data whenever possible. Although numerous studies on baboon communication have been reported, sonograms for this species are apparently lacking in the published literature. Communication studies involving spectrographic analysis have also been reported on several other species, such as those of Reynolds (in Marler, 1965) on the chimpanzee, Schaller (1963) on the gorilla, Moynihan (1964) on the night monkey, Altmann (1967) on howlers, Ploog (1966) on squirrel monkeys, Petter and Petter (1966) on the aye-aye, and Petter (1962) on lemurs. For a more complete listing of studies on primate communication, spectrographic or otherwise, the reader is referred to Altmann's (1968) comprehensive review.

Although Old World monkeys have been extensively studied in terms of behavior and communication, several genera within the family Cercopithecidae have not been adequately investigated. Among these are the species of the genera Cercopithecus and Colobus.

Other than Struhsaker's (1967) study on the vervet, Cercopithecus aethiops, and most recently his investigations of the vocalizations of several Cercopithecus species (1970), very little information on vocalizations is available for the Cercopithecus group. Most of what is known of the auditory communication of these species has been drawn out of more general behavioral studies or from anecdotal accounts. Other researchers on the vervet include Booth (1962), Gartlan and Brain (1968), and Hall and Gartlan (1965). None of these studies presents spectrographic descriptions. The redtail monkey, C. ascanius, is the only other species investigated to any extent and the reader is referred to the works of Buxton (1952) and Haddow (1952). Again, spectrographic data is not available for this species in these studies.

Very little is known of the behavior of the Colobus species. While considerable research has been carried out on the Asiatic counterpart of the Colobinae, the langurs, the African members of this subfamily have been largely ignored. Available reports include those of Booth (1957) on the olive colobus and Hill and Booth (1957) and Ullrich (1961) on the black and white colobus. However, information as to social communication is rather sparse and incomplete in these studies. A more informative study is Marler's (1970) spectrographic analysis of the vocalizations of the red colobus.

Objectives of the Present Study

In the present study the vocalizations of two species of these relatively little-studied genera, the Sykes monkey, Cercopithecus mitis kibonotensis, and the black and white colobus monkey, Colobus polykomos palliatus, will be described and analyzed. The basic aim of this study is to present a catalogue of the vocal repertoire of these species. Accompanying behavioral information will also be presented whenever available.

The vocalizations of the baboon, Papio cynocephalus, will also be described. This investigation formed part of a larger study being conducted at the time by William R. Maples, William F. Greenhood, and myself on crop-raiding behavior of baboons. The aim of this portion of that study is to describe those vocalizations given while crop-raiding and to investigate the role they play in this activity.

All descriptions and classifications of the calls are based on spectrographic analysis.

The Study Sites

The field observations upon which the following study is based were conducted in Kenya, East Africa, from September to December, 1969. The study site for the Sykes and colobus monkey material was at Diani Beach on the Kenya coast, approximately eighteen miles south of Mombassa. The site itself was approximately one-quarter to one-half mile inland. The

material on baboon vocalizations was collected at farm sites primarily at Shimoni, a small fishing village near the southern tip of the Kenya coast. Some recordings were also made near Roka along the Mombassa-Malindi road, approximately twenty-four miles south of Malindi.

In general, the climax vegetation community for the Diani Beach/Shimoni area has been described as lowland dry forest on coral rag (Combretum schumanii-Cassipourea species) (Moomaw, 1960). The forests at Diani Beach are broken into smaller segments of varying size by the interspersal of lantana thicket and cultivated land. The forest essentially consists of two layers, an upper canopy composed of tall, branching trees and a low, dense understory where bushes and vines predominate. The colobus were observed to favor the upper canopy but would readily take refuge in the lower layer when necessary. The Sykes seemed equally at home in both layers but it was this observer's impression that more time was spent in the understory. At Roka, the baboons inhabited a protected forest which has been classified as lowland woodland (Brachystegia-Afzelia species) by Moomaw (1960). For a more detailed discussion of the ecology of these areas and the species of vegetation which predominate, the reader is referred to Moomaw (1960) and Greenhood (1971).

Methods and Materials of Research

Recordings of the vocalizations were made with a Nagra IV L portable tape recorder at 15 ips with a frequency

response of 30 to 20,000 cps, and a Sennheiser directional microphone, Model MKH 804. Sonograms for analysis were made on a Kay Electric Sona-Graph, Model 6061-B. A transparent plastic grid overlay was made showing time on the horizontal axis and frequency on the vertical axis. The grid was placed over the sonograms and approximate frequency and temporal measurements were taken.

Field recording techniques at Diani Beach consisted of approaching as closely and quietly as possible on foot a Sykes or colobus troop. The thick, tangled vegetation of this area precluded any possibility of following a troop on its daily movements; therefore, recordings were made along roads and footpaths which troops regularly frequented and traversed. At Shimoni, a stationary recording site was set up within the farm and baboon vocalizations were recorded as the troops approached and entered the field to raid. The recording station at the Roka site was within an observation vehicle which would follow and remain adjacent to the movements of a troop of crop-raiding baboons as they emerged from the forest and crossed the Malindi-Mombassa road to raid the farms on the other side. In all cases, accompanying behavioral observations were recorded in a notebook.

In areas of limited visibility it was the observation of behavioral context which proved to be the most difficult. A single individual attempting to operate a tape recorder, direct a microphone, maintain visual contact with a troop moving in dense underbrush, and take notes is limited as to

the amount of behavior which can be observed. This limitation was particularly felt in the Diani Beach area. At Shimoni and Roka the problem was not as acute as other workers (notably William R. Maples) were simultaneously observing crop-raiding behavior and so correlation of the vocalizations with their observations was possible. It would seem, therefore, that perhaps the most fruitful means of studying communication with all its behavioral ramifications within a somewhat hostile environment would be through a team approach. Such a system would minimize the physical limitations and would facilitate the recording of observations. In addition, it would provide a system of checks and counter-checks on what was observed. Perhaps in savanna areas, with visibility relatively unimpaired, these difficulties do not pose as serious a hinderance as when dealing with forest populations. In the latter case, the physical limitations imposed by the very nature of the study itself are only too apparent.

Definition of Terms

So that there may be some form of common reference in discussions of primate vocalizations, use will be made here of the terms defined by Thomas T. Struhsaker in his study on auditory communication of vervet monkeys. These are as follows:

Unit: The unit is the basic element of a call, and is represented as a continuous tracing along the temporal (horizontal) axis of the sonogram.

Phrase: The phrase is a group of units that is separated from other similar groups by a time interval greater than any time interval separating the units within a phrase.

Bout: A bout is a grouping of one or more phrases separated from other similar groupings by a time interval greater than that separating any of the phrases within a bout.

Nontonal unit: A nontonal unit is composed of sound that is more or less continuously developed over a wide range of frequencies. This has also been called "noise" by Andrew (1963b) and "harsh noises" by Rowell and Hinde (1962).

Tonal unit: A tonal unit is composed of sound characterized by one or more relatively narrow frequency bands and has been referred to as "clear calls" by Rowell and Hinde (1962) and "sound" by Andrew (1963b). Units with a harmonic structure are included in this category.

Compound unit: A compound unit is composed of both nontonal and tonal sounds that appear as a continuous tracing on the sonogram.

Mixed unit: Units composed of both tonal and nontonal sounds that are rather superimposed on one another are called mixed units. The tonal and nontonal aspects are more or less separated by differences in frequency.

Distribution of major energy of nontonal sounds: The distribution of the major energy of a nontonal sound is represented and thus determined by the darkest portion of the tracing on the sonogram. This distribution is generally over a smaller range than the frequency range of nontonal sounds. The distribution of major energy of nontonal sounds is described by an upper frequency (highest pitch of major energy) and a lower frequency (lowest pitch of major energy). (Struhsaker, 1967:282-283)

For a brief demonstration of how these terms will be applied in the present study, the reader is referred to Figure 26 and Figure 6.

Figure 26 is a spectrographic representation of a colobus vocalization consisting of three different phrases.

The first is a nontonal, single-unit phrase and is given only once at the beginning of the call. The second phrase consists of several tonal units. The third is a nontonal, single-unit phrase very similar to the first. The second and third phrases are repeated in alternation. All three phrases are said to form a bout, part of which is depicted in the sonogram. The entire bout can be referred to as a "call" or "vocalization".

Figure 6 represents a call of Cercopithecus mitis and can be described as a single-unit phrase. It is also a compound unit since a brief tonal component consisting of gently arching frequency bands is followed by a noise or nontonal component with a somewhat irregular appearance on the sonogram.

For a further demonstration of how these terms are used, the reader is referred to the descriptions of the various calls presented in the text which can be compared with the appropriate sonogram.

CHAPTER II

VOCALIZATIONS OF THE SYKES MONKEY

The Sykes monkeys (Cercopithecus mitis kibonotensis) live in social groups of substantial size. Various troop counts, made while the monkeys passed over an "arboreal bridge" spanning a roadway, revealed totals of 13, 18, 26, and 31. However, it never was clear how many troops were involved or if an entire troop had been counted. Sykes are primarily an arboreal species but, as mentioned previously, seem to be equally at home in the tall trees as in the lower brush. They seem not the least bit reluctant to move along on the ground, especially in those areas where the vines are quite thick and tangled.

The Sykes would vocalize quite readily. The chirp was the most frequently heard call and would be elicited by any sudden movement or noise, or by the approach of humans or dogs. In the initial stages of the study, the observer was constantly the object of much threat behavior and chirping. However, as the Sykes became habituated to the observer's presence and with the thickening of the foliage due to rain, the amount of vocalizations given was considerably reduced.

Classification of CallsChirp

The chirp (Figs. 1&2 and Table 1) was given by adult females and immature monkeys and possibly by adult males, although positive identification of the latter was not possible. That adult male Sykes might give the call is doubtful in light of Struhsaker's (1967, 1970) reports for the vervet and other Cercopithecus species in which he noted that chirps were not given by adult males.

The chirp was an abrupt, sharp-sounding call of high frequency and short duration. The frequency range was 0.10 - 16.0+ kHz but the average distribution of the major concentration of energy was 2.91 - 6.14 kHz (N=29). Sonograms revealed a single-unit phrase with an abrupt beginning consisting of a narrow, tonal, chevron-shaped component followed by a noise component of longer duration. The noise component of approximately half of the chirps was distributed in a two-band arrangement, while the other half consisted of a single, broader band (Figs. 1&2). The mean duration of the chirp was 0.18 seconds (N=29).

The chirp apparently functions as a threat-alarm call. It is usually given in conjunction with a threat display in which the monkey either crouches forward with legs stiff and bobs its head and shoulders up and down, or else lunges forward on its forelimbs. In both cases the monkey stares intently at the intruder. This behavior was directed toward dogs and humans but never was observed between one Sykes and

another. A similar observation was made by Haddow (1952) in his study on the redbellied monkey, Cercopithecus ascanius.

TABLE 1

CHIRP

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	29/29	1.00	1.00-1.00
Phrase Duration (secs.)	29	0.18	0.10-0.25
Lower Limit of Major Energy (kHz)	29	2.91	1.50-4.00
Upper Limit of Major Energy (kHz)	29	6.14	3.00-8.00

Chirps were also given by a feeding animal, the feeding in some instances being an apparent nervous displacement activity but on other occasions a true feeding activity.

The frequency of repetition of the chirps was variable as was the intensity of the call. Some chirps were given loudly and in rapid succession; for example in response to a loud, sudden noise or to a dog passing nearby. On other less tense occasions chirps were given infrequently and softly, almost whisper-like.

Other Sykes responded to the chirping animal by looking in its direction and in the direction of its threat and by chirping also. Occasionally the other animals would move deeper into the brush but this was not necessarily a hurried

retreat. In some instances the only Sykes remaining visible was the chirping individual who would soon move off and join the others.

Multiple Chirps

Included in the Sykes' repertoire in addition to the single-unit chirps are two- and three-unit chirps (Figs. 3-5 and Table 2). Such multiple chirps were also reported by Struhsaker (1970) for Cercopithecus cebus, C. erythrotis, and C. nictitans. As is the case for single chirps, multiple chirps are apparently restricted to adult females and immature monkeys.

In the two-unit chirp, the distribution of major energy in the second unit is over a greater range (2.84 - 5.96 kHz) than in the first (3.80 - 5.96 kHz). This distinction was also made by Struhsaker (1970) for the three Cercopithecus species listed above. Struhsaker found that this shorter frequency range of the first unit was due both to a higher lowest frequency and a lower upper frequency. However, in the case of C. mitis only the lowest frequencies were found to differ considerably. That is, in 88.9 percent of the double chirps the lowest frequency of Unit I was higher than the lowest frequency of Unit II, whereas the upper frequencies of the two units were the same in 66.7 percent of the calls (N=9).

Generalizations concerning energy distribution for the three units of the triple chirp can not be made since only one such call was recorded. However, in this one case energy distribution increased with each subsequent unit.

TABLE 2
MULTIPLE CHIRP

		Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase				
Double		18/9	2.00	2.00-2.00
Triple		3/1	3.00	3.00-3.00
Unit Duration (secs.)				
Double	Unit I	9	0.06	0.05-0.08
	Unit II	9	0.20	0.12-0.28
Triple	Unit I	1	0.05	0.05-0.05
	Unit II	1	0.08	0.08-0.08
	Unit III	1	0.25	0.25-0.25
Interval Between Units (secs.)				
Double		9	0.00	0.00-0.00
Triple		2	0.03	0.05-0.01
Phrase Duration (secs.)				
Double		9	0.25	0.18-0.32
Triple		1	0.44	0.44-0.44
Lower Limit of Major Energy (kHz)				
Double	Unit I	9	3.80	3.00-5.00
	Unit II	9	2.84	2.00-3.60
Triple	Unit I	1	2.00	2.00-2.00
	Unit II	1	2.00	2.00-2.00
	Unit III	1	2.00	2.00-2.00
Upper Limit of Major Energy (kHz)				
Double	Unit I	9	5.95	5.50-7.00
	Unit II	9	5.95	5.00-7.00
Triple	Unit I	1	3.00	3.00-3.00
	Unit II	1	3.50	3.50-3.50
	Unit III	1	5.00	5.00-5.00

In addition to frequency differences, the durations of the two units of the double chirp also differ, with the first unit being shorter than the second in all cases. The durations of the units of the three-unit chirp also increase from first to third, but again any generalization must await a larger sample.

It is interesting to note that in both energy distribution and duration the final units of both the two- and three-unit chirps fall within the range of values for the single-unit chirp.

Nyah and Short Nyah

The nyah (Fig. 6 and Table 3) is a loud call consisting of tonal and nontonal components. Although the call itself consists of a single-unit phrase, it always occurred in bouts in which it was repeated at intervals of approximately 0.50 seconds.

On the sonogram the nyah appears as a harmonic series of bands beginning abruptly and arching into a mixed band of tonality and noise. In a variant of the nyah, referred to here as the short nyah (Figs. 7&8 and Table 4), this harmonic band pattern at the beginning is absent, the call, therefore, sounding like a sharp "ah". Both the nyah and the short nyah can be given in a bout, but it seems the latter was usually given under tense or excitable conditions, such as a pack of stray dogs passing nearby.

Mean duration for the nyah was 0.31 seconds (N=12) and 0.19 seconds for the short nyah (N=14). The average

energy distribution for both forms was quite similar, with 0.82 - 5.46 kHz for the nyah (N=15) and 0.57 - 5.31 kHz for the short form (N=14). Total energy distribution ranged from 0.10 - 16.0+ kHz for both calls. Since it was never known exactly how many Sykes groups were in the area and since individual groups were not distinguishable, it is possible that all the nyahs of the sample were made by the same individual. This possibility is based on the assumption that there is but one adult male per group, a common occurrence among Cercopithecus monkeys according to Struhsaker (1969). The short nyahs of the sample, however, were given by one individual only since they were all recorded on a single occasion with only one troop present.

TABLE 3

NYAH

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	15/15	1.00	1.00-1.00
Phrase Duration (secs.)	12	0.31	0.20-0.38
Lower Limit of Major Energy (kHz)	15	0.82	0.25-1.80
Upper Limit of Major Energy (kHz)	15	5.46	4.00-7.00

TABLE 4
SHORT NYAH

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	14/14	1.00	1.00-1.00
Phrase Duration (secs.)	14	0.19	0.05-0.28
Lower Limit of Major Energy (kHz)	14	0.57	0.20-2.30
Upper Limit of Major Energy (kHz)	14	5.31	4.00-6.50

The animal giving the call was very difficult to observe; in fact, this was done on only one occasion and quite by accident. A single Sykes was observed sitting alone in the topmost branches of a tall tree giving the call at about 18:00. No other Sykes were visible in the immediate area. The call was made by exhaling forcibly with the mouth open. This individual was too far away to permit accurate sexual identification but its large size would indicate it to be most likely a male. This assumption is further supported by Haddow's (1952) observation of the redtail monkey, C. ascanius, in which only the adult male gives a call Haddow described as "Kyuh". In addition, the nyah and short nyah of the Sykes are probably equivalent to the "loud calls" reported by Struhsaker (1970) and Bourliere, Hunkeler, and Bertrand (1970) for other Cercopithecus species which were also only given by adult males.

Struhsaker's (1970) "loud calls" are of two types, the pow and the hack. Since he does not make explicit the basis for distinguishing them spectrographically, and since he does not do so in his table of measurements, it is impossible to compare or correlate one or the other with the nyah or short nyah.

The nyah call was frequently given prior to group progression. It may have signaled group withdrawal, for soon after the call was given no Sykes would be visible in the area, having moved in the direction from which the call came. In addition, such calls seem to be evoked by a potentially disruptive or threatening stimulus as was the case with the pack of dogs. Bourliere, Hunkeler, and Bertrand report that loud calls are given by the alpha male in the evening at the sleeping trees and also "in response to any situation that was potentially dangerous for the group members, or potentially disruptive to the cohesion of the group" (1970:313). Haddow (1952) and Struhsaker (1969) concluded that the loud calls may function as a central focal point for maintaining intragroup cohesion on occasions when the group might be dispersed and may also function in intergroup spacing.

Boom

On several occasions a low frequency call was heard which sounded very much like "whoo" but which closely resembles in frequency and duration the booms of the mona super-species as described by Struhsaker (1970). The boom (Fig. 9 and Table 5) is completely tonal and appears as a very

black band situated at the bottom of the sonogram. The call is given as a single-unit phrase, is seldom repeated, and appears to be strikingly uniform.

The energy distribution is restricted to such a low frequency that the lowest distribution of energy on the sonogram is difficult to read, being so close to the bottom margin of the sonogram itself. This lower limit of the energy range has, therefore, been approximated at 0.01 kHz. The upper limit of energy distribution is 0.40 kHz (N=2).

TABLE 5

BOOM

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	2/2	1.00	1.00-1.00
Phrase Duration (secs.)	2	0.20	0.20-0.21
Lower Limit of Energy (kHz)	2	0.01	0.01-0.01
Upper Limit of Energy (kHz)	2	0.40	0.40-0.40

The individual giving the call was never seen, nor did the animal sound as if it were very close to the observer. However, among those species (Cercopithecus mona, C. campbelli, and C. pogonias) which Struhsaker (1970) studied that had boom calls, only adult males gave the call.

Apparently, the boom was involved in some way with coordinating group movement as it was usually given while the

group was moving, or else the group would move soon thereafter. On several occasions the boom was heard following agonistic encounters within the group and so may serve to facilitate group cohesion by overriding the disruptive and dispersive effects of antagonism among its members.

Squeal

The squeal (Fig. 10 and Table 6) was a high-pitched, uniform call. It is entirely tonal and occurs as a single-unit phrase. On the sonogram the squeal appears as two slightly undulating bands, one at approximately 3.00 - 4.00 kHz and the other at 6.00 - 7.50 kHz. The end of the call lies on a slightly lower frequency level than the beginning.

TABLE 6

SQUEAL

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	7/7	1.00	1.00-1.00
Phrase Duration (secs.)	7	0.63	0.39-1.20
Lower Limit of Energy (kHz)	7	3.20	2.70-3.50
Upper Limit of Energy (kHz)	7	7.87	7.00-9.00

The mean duration of the squeal is 0.63 seconds (N=7). The mean lower frequency is 3.20 kHz and the mean upper frequency is 7.87 kHz (N=7).

Shriek

The shriek (Fig. 11 and Table 7) was a high-pitched, shrill-sounding call of variable duration. Certain sections of the call vary in degree of tonality and duration. Since it appears as a continuous tracing on the sonogram it must be classed as a compound, single-unit phrase.

The first part of the shriek resembles the squeal and is completely tonal with a two-band appearance on the sonogram. However, it is somewhat higher in pitch than is the squeal, with a mean frequency of 3.46 - 8.74 kHz (N=5). This first part continues into, and is superimposed by, a mixed tonal-nontonal portion which appears as a noisier, broader, double band with a mean frequency of 3.20 - 8.64 kHz (N=5). As the call progresses, this portion may become noisier and its appearance will become more distorted on the sonogram.

The mean duration of the tonal component is 0.36 seconds (N=5), while that of the mixed portion is 0.65 seconds (N=5) for a mean total phrase length of 1.01 seconds.

Chut

On one occasion a call was given which can perhaps best be described as sounding like "chut" (Figs. 12&13 and Table 8). There were three such chuts or units grouped together to form a phrase and two phrases were given. There is some tonal quality to the call but this is overlapped for the most part by a nontonal component (thus forming a mixed unit) giving the call a noisy appearance on the sonogram.

TABLE 7

SHRIEK

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	5/5	1.00	1.00-1.00
<u>Tonal Portion</u>			
Duration (secs.)	5	0.36	0.13-0.55
Lower Limit of Energy (kHz)	5	3.46	3.10-4.00
Upper Limit of Energy (kHz)	5	8.47	7.50-9.50
<u>Mixed Portion</u>			
Duration (secs.)	5	0.65	0.27-0.99
Lower Limit of Major Energy (kHz)	5	3.20	3.00-3.50
Upper Limit of Major Energy (kHz)	5	8.64	8.00-9.00

The mean unit duration was 0.08 seconds (N=6) and the average distribution of major energy was 2.95 - 4.53 kHz (N=6). However, of the three units the third was the longest (0.12 seconds) and had a greater frequency range. The upper limit of the total energy range of this third unit was approximately 13.0 kHz. On the sonogram the first unit appears as a single band while the second and third units consist of two bands. However, the second of these bands is difficult to discern and measure since it is considerably obscured by the noise component. Although there are some spectrographic similarities with the chutter, the calls differ enough acoustically to warrant their separate classification at this time.

TABLE 8

CHUT

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	6/2	3.00	3.00-3.00
Unit Duration (secs.)	6	0.08	0.03-0.13
Interval Between Units (secs.)	4	0.12	0.05-0.20
Phrase Duration (secs.)	2	0.50	0.49-0.50
Lower Limit of Major Energy (kHz)	6	2.95	2.50-3.50
Upper Limit of Major Energy (kHz)	6	4.53	3.20-5.50

The chut was given by either a subadult or small adult, possibly female. Two such animals were grooming high up in a tree. Upon seeing the observer, the one being groomed gave a squeal which was followed by the chut phrases. It then moved away from the groomer who chirped when it noticed the observer. Taking into consideration the context in which it was given and the call with which it was associated, the chut could be tentatively identified as a fear-alarm call.

Chutter

The chutter (Fig. 14 and Table 9) is a completely nontonal phrase composed of several units of short duration. Each unit on the sonogram resembles a column of noise with some broader than others. There is some variation in chutter phrase duration, depending upon the number of units included in the call. One of the three calls sampled contained twelve units, the others each had four. The significance of phrase length differences is not yet understood, but perhaps there is some relationship between the intensity of stimulus arousal and the number of units per phrase. It is also possible that the variation reflects individual differences. Perhaps more than one type of chutter is represented in the sample. Struhsaker (1967) was able to discern several different kinds of chutters for the vervet monkey. Without a larger sample size and more information as to the function of the chutter calls and the circumstances which evoke them, any statement as to a possible typology of chutter phrases would be premature.

The unit duration and the interval between units was similar among the three phrases. However, it was noticed that the units of a phrase tend to increase in duration and intensity such that those units late in the phrase are the longest and loudest. The major energy distribution ranged from 2.00 - 11.00 kHz with the mean distribution as 2.67 - 7.83 kHz (N=18).

TABLE 9

CHUTTER

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	20/3	6.33	4.00-12.00
Unit Duration (secs.)	18	0.06	0.01-0.11
Interval Between Units (secs.)	15	0.04	0.01-0.08
Phrase Duration (secs.)	3	0.58	0.39-0.95
Lower Limit of Major Energy (kHz)	18	2.67	2.00-4.00
Upper Limit of Major Energy (kHz)	18	7.83	4.00-11.00

The individual giving the chutter call was never seen and the situations in which they were given were seldom apparent. They were sometimes, but not always, heard during intragroup fights so apparently the chutters play some part in agonistic encounters. Struhsaker (1959) likewise reports

having heard chutters during the fight episodes of other *Cercopithecus* species.

Low, Short Chutter

On one occasion a low chutter of short duration (Fig. 15 and Table 10) was given by an adult Sykes. Two phrases were recorded, each consisting of two units. This chutter is lower in frequency than the chutter described above, with a mean major energy distribution of 0.75 - 2.88 kHz (N=4). However, in terms of total energy distribution, there is some indication on the sonograms of energy in the vicinity of 7.50 kHz.

TABLE 10
LOW, SHORT CHUTTER

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	4/2	2.00	2.00-2.00
Unit Duration (secs.)	4	0.04	0.03-0.07
Interval Between Units (secs.)	2	0.05	0.05-0.05
Phrase Duration (secs.)	2	0.14	0.13-0.15
Lower Limit of Major Energy (kHz)	4	0.75	0.50-1.00
Upper Limit of Major Energy (kHz)	4	2.88	2.75-3.00

Energy distribution and duration of each of the units are quite similar, with the units appearing on the sonograms as thin columns of noise. Mean unit duration is 0.04 seconds ($N=4$) and phrase duration averages 0.14 seconds ($N=2$). This chutter, like the previous one, is entirely nontonal.

Chutter-Squeal

The chutter-squeal (Figs. 16-18 and Table 11) can best be described as a multi-phrase bout of long duration. The following discussion is based on measurements of two such calls which were both recorded during the same session. Since the vocalizing individual was not seen, it is possible that both these calls were given by the same animal.

The first phrase consists of a series of short units resembling in some ways both the chutter and the chirp. These units are basically nontonal like the chutter but yet there is a hint of a chevron-shaped tonal component (as in the chirp) superimposed over the nontonal element. The first bout had a phrase consisting of nine chutter units and the second bout had four chutter units. With a mean unit duration of 0.07 seconds ($N=13$), the units are as short as those of the chutter but do not have as wide a frequency range.

Shortly following this first phrase are single-unit phrases which appear on the sonogram as nontonal-tonal undulating bands. There were five of these phrases in the first bout and two in the second. These phrases are of long duration; two sampled had a mean duration of 3.93 seconds. The

mean of the lower frequency of major energy distribution is 3.75 kHz while the mean upper frequency is 7.00 kHz.

The final phrase of the bout is also a single, mixed, tonal-nontonal unit but the nontonality or noise is not as pronounced as in the preceding phrases. The average duration of this unit is 0.62 seconds (N=2) and the mean frequency range is 3.25 - 5.65 kHz (N=2).

TABLE 11
CHUTTER-SQUEAL

	Number (N)	Mean (\bar{x})	Range (R)
<u>Chutter Portion</u>			
Units/Phrase	13/2	6.50	4.00-9.00
Unit Duration (secs.)	13	0.07	0.02-0.10
Interval Between Units (secs.)	11	0.04	0.02-0.08
Phrase Duration (secs.)	2	0.64	0.39-0.88
Lower Limit of Major Energy (kHz)	13	3.15	2.50-4.50
Upper Limit of Major Energy (kHz)	13	5.94	4.00-7.00
<u>Mixed Portion I</u>			
Interval Between Chutter & Mixed I (secs.)	2	0.02	0.02-0.03
Units/Phrase	2/2	1.00	1.00-1.00
Phrase Duration (secs.)	2	3.93	3.08-4.78

TABLE 11 (Continued)

	Number (N)	Mean (\bar{x})	Range (R)
Lower Limit of Major Energy (kHz)	2	3.75	3.50-4.00
Upper Limit of Major Energy (kHz)	2	7.00	6.50-7.50
<u>Mixed Portion II</u>			
Interval Between Mixed I & Mixed II (secs.)	2	0.14	0.10-0.18
Units/Phrase	2/2	1.00	1.00-1.00
Phrase Duration (secs.)	2	0.62	0.50-0.73
Lower Limit of Major Energy (kHz)	2	3.25	3.00-3.50
Upper Limit of Major Energy (kHz)	2	5.65	5.50-5.80
<u>Total Duration</u>	2	5.35	4.10-6.60

Neither the final nor preceding phrases show any great similarity, audibly or spectrographically, to the shriek or saueal phrases reported earlier.

The sum of the duration of each of the phrases as well as the intervals between them results in a lengthy call averaging approximately 5.35 seconds (N=2).

Growl

The growl (Figs. 19&20 and Table 12) is predominately a tonal call although there may be some nontonality present, particularly at the end of the vocalization. The growl consists of a multi-unit phrase which may occur singly or may be repeated.

TABLE 12

GROWL

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	135/17	7.94	3.00-20.00
Unit Duration (secs.)	135	0.02	0.01-0.03
Interval Between Units (secs.)	118	0.02	0.01-0.03
Phrase Duration (secs.)	17	0.20	0.05-0.59
Interval Between Phrases (secs.)	9	0.49	0.08-0.67
Lower Limit of Major Energy (kHz)	17	0.52	0.25-0.75
Upper Limit of Major Energy (kHz)	17	1.15	1.00-2.00

The number of units per phrase was variable but averaged 7.94 units per call (N=17). The unit duration and the interval between units was similar in all the phrases sampled, so phrase duration was largely dependent on the number of

units present. Since the number of units varied from three to twenty, phrase duration varied considerably also. However, the mean phrase duration was 0.20 seconds (N=17). Despite their temporal variation, the calls are grouped into a single category at this time on the basis of their acoustic and spectrographic similarities.

Energy was distributed on approximately half the sonograms in a single band formation (N=8) and in a double (N=5) or triple (N=4) band arrangement on the remainder. In the last two cases, however, most of the energy would be concentrated in the lowermost band. The average distribution of the heaviest energy concentration, therefore, was 0.52 - 1.15 kHz (N=17) but the total energy distribution might extend to 3.50 kHz in some cases.

Identification of the vocalizing individual was difficult but the call was apparently given by both juveniles and adults. Examples of instances when the growl was heard include: during chirping sequences by a Sykes threatening the observer, as Sykes fed while looking at the observer, during fight episodes, and while a troop was moving in the brush.

Err

A call somewhat similar acoustically to the growl is the "err" (Fig. 21 and Table 13). On the sonogram, however, each call is broken into four or five short, discrete units which extend to higher frequency levels than the growl. The "err" is completely tonal.

The mean phrase duration of the "err" is 0.17 seconds (N=3), with a mean energy range of 0.81 - 5.25 kHz for the units (N=14).

TABLE 13

ERR

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	14/3	4.67	4.00-5.00
Unit Duration (secs.)	14	0.02	0.01-0.05
Interval Between Units (secs.)	11	0.02	0.01-0.05
Phrase Duration (secs.)	3	0.17	0.12-0.28
Lower Limit of Energy (kHz)	14	0.81	0.50-1.20
Upper Limit of Energy (kHz)	14	5.25	4.00-7.50

The individuals vocalizing were not identified and the function of the "err" call is not understood. However, the call was heard immediately following a shriek on two of three occasions.

Uh

A short call best described as sounding like "uh" (Fig. 22 and Table 14) was given before a shriek three times out of a sample of five. The call was given in pairs or in threes with a mean interval between the units of 0.12 seconds

(N=7). The mean unit duration was very short at 0.04 seconds (N=12).

TABLE 14

UH

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	12/5	2.40	2.00-3.00
Unit Duration (secs.)	12	0.04	0.01-0.09
Interval Between Units (secs.)	7	0.12	0.04-0.24
Phrase Duration (secs.)	5	0.28	0.08-0.40
Lower Limit of Major Energy (kHz)	12	1.78	1.00-3.50
Upper Limit of Major Energy (kHz)	12	5.56	4.10-8.00

The "uh" is lower in frequency than the shriek which sometimes followed (three out of five times). The mean lower frequency of major energy is 1.78 kHz and the mean upper frequency is 5.56 kHz (N=12). The call is entirely nontonal and appears as a narrow column of noise on the sonogram.

Discrete and Graded Signals

In a study such as this in which the vocal repertoire of a primate species is being classified and described, it is customary to examine the nature of the signals as to

whether they are discrete or graded. Discrete signals are separate and distinguishable whereas graded signals are more variable and can be arranged to form a continuum with other such signals.

Marler has pointed out that continuous or graded sounds are more common in rhesus monkeys, baboons, chimpanzees, and gorillas, resulting in sound systems which are "much more complex in the development of these subtle continuous and multidimensional variations of the sound signals" (1965:566). The graded nature of the vocalizations of these terrestrial or semi-terrestrial species which are relatively isolated from other primate species of similar size and structure contrasts significantly, says Marler, with the relatively discrete nature of the sound systems of forest-living primates in frequent contact with other primate species, such as is the case with Cercopithecus and Colobus.

In such circumstances the possibility of inter-specific confusion is greatly increased and, correspondingly, the limited evidence available on the sound signals of such forms suggests that they are more highly structured and that this structuring is used at least in part to maintain species specificity in a major proportion of the vocal repertoire. (Marler, 1965:565)

The vocal repertoire of the Sykes monkeys seems to comply with Marler's thesis. In the study area there were three other diurnal species of nonhuman primates observed, the baboon (Papio cynocephalus), the colobus (Colobus polykomos), and the vervet (Cercopithecus aethiops). The Sykes were at times observed in close proximity to all three species. Of these species, the vervet is the most closely

related to the Sykes, morphologically and behaviorally. According to Struhsaker (1967), the majority of the vervet vocalizations which he studied were of the discrete type. Similarly, most of the Sykes' calls, while showing some degree of variability within categories, are also of the discrete type. Signals which may prove to be of the continuous type would include the shriek and the squeal, and the calls of the chutter group.

For example, the squeal was described as a tonal call consisting of two parallel bands with a mean energy distribution of 3.20 - 7.87 kHz (N=7). The shriek, on the other hand, was composed of two components, a two-band tonal section followed by a mixed portion of tonal and nontonal sound. The initial tonal component strongly resembles the squeal, but the mean energy distribution is slightly higher at 3.46 - 8.74 kHz (N=5). However, the ranges for the energy values for the two calls do overlap (Table 6 and Table 7). It would seem likely, therefore, that there may be a graded continuum between squeals and shrieks.

There may also be a continuum within the chutter group, although the sample is small and hence not extremely reliable. Perhaps the chut, the chutter, and the short chutter are but points along a graded continuum of such calls. Also, there may be some functional significance in the number of units per chutter phrase, creating a gradient in this regard as well.

Future fieldwork and further study may point out more continuous signals for the Cercopithecus mitis group as well as modify those tentatively identified here.

This investigation has demonstrated the possible existence of a graded series of signals or messages. That this is not sufficient evidence to indicate a graded communication system has been aptly pointed out by Altmann (1967). He stresses that signals used in graded or analogical communication must be differentiated from those signals which may appear graded but merely reflect the normal range of variation which a sample of calls may be expected to show. Such variation would be due to the morphological and physiological variations of the structures involved in sound production. It is necessary, says Altmann, to demonstrate functional continuity: "What is needed is (1) a continuous array of messages, (2) a continuous array of responses to these messages, and (3) a one-to-one mapping between messages and responses" (1967:341).

The failure to make the distinction between graded signals which are associated with graded responses and those which are not has resulted in some confusion and misunderstanding concerning the use of the terms 'discrete' and 'graded'. The terms were introduced into the study of primate communication largely through the work of Hockett (1960) who proposed thirteen design features, of which discreteness was one, which he felt were characteristic of human languages. Apparently in their haste to look for Hockett's design features among the communication systems of nonhuman

primates, many researchers failed to recognize that discreteness and gradedness among the response patterns as well as discreteness and gradedness among the signals themselves must be demonstrated in order for a communication system to be classified as one or the other. Consequently, although these terms occur frequently in the literature, Altmann (1967) points out that a graded communication system has never been demonstrated. Even if such a system were described, Altmann further emphasizes that discontinuities between the major categories of communication patterns themselves will make for a certain amount of discreteness. The classification of the system as one or the other, therefore, largely becomes a question of semantics.

It would seem that an understanding of the nature of communication systems among nonhuman primates lies not in its comparison, feature for feature, with human language but rather with the understanding of the adaptive significance of such features as may be present. That the latter has not yet been accomplished is due in large part to the fact that primate communication studies are still in their infancy. Hopefully, however, through future field studies and the amassing of greater amounts of information, certain adaptive trends and correlations will become apparent which will have significance for understanding not only the nature of nonhuman primate communication but the nature of human language as well.

A Structural-Functional Analysis

There are many different types of vocalizations among the primates and these vocalizations serve various functions. However, the exact nature of the relationship between function and structure of primate calls has not yet been determined. Although work along these lines has been carried out for some insect species (Alexander, 1960, 1968), anuran species (Bogert, 1960; Littlejohn, 1959), and avian species (Marler, 1955, 1959; Marler and Hamilton, 1966), most discussions of primate vocalizations in structural-functional terms have remained generalized.

There are several reasons which may account for these generalized studies. Firstly, the study of primate communication is still a relatively new endeavor and the emphasis, until recently, has been on collection and description rather than on detailed investigative analysis. Secondly, primate communication has been shown to be an exceedingly complex process involving several channels of communication; namely, visual, auditory, tactile, and olfactory. The relative contribution which each of these channels makes to a species' communication system, the degree to which they are interrelated, and the extent to which they limit and modify communication by other channels are difficult to assess. Therefore, a discussion of the structure of a particular vocalization must also account for the possibility of simultaneous transmission of information by some other means, such as visual signals. Thirdly, the determination of the function of a call is often

difficult, requiring an evaluation of the behavioral and environmental contexts in which the call was given as well as a description of the nature of the responses which it evoked. Consequently, among those primate species which have been studied, there remain numerous calls whose functions are unknown. Lastly, it has not yet been determined which aspects of a primate vocalization, if any, are most significant for the transmission of information. That some components of a call, such as frequency, intensity, duration, and timing, are differentially informative has been shown to be the case among arthropods (Alexander, 1968), anurans (Bogert, 1960), and birds (Falls, 1963; Marler, 1955, 1959). Experimental designs, such as play-back techniques both in the laboratory and in the field, will probably be of considerable importance in evaluating the communicative significance of the various components.

The present investigation will attempt to apply a structural-functional approach to the study of Sykes vocalizations by focusing on several principles of sound localization as outlined by Marler (1955, 1959) in his studies on bird vocalizations. Structural comparisons will be made between those Sykes calls used to communicate over long distances and those which operate at close range. The discussion will be limited to those calls whose functions are known.

As Marler (1955, 1959) points out, sound localization in vertebrates relies on binaural comparisons of differences in phase, intensity, and time of arrival. Intensity differences become apparent when the head acts as an obstruction,

thus hindering the sound from reaching one ear. The direction of the sound can be inferred due to the resulting difference in intensity at the two ears. Since this "shadowing effect" is significant only when the obstruction is of the same order of size as the sound wavelength or larger, localization by intensity differences is most useful with high frequency sounds (Marler, 1959).

On the other hand, localization by phase differences is confined to low-pitched sounds (Marler, 1959). Phase differences are the result of pressure changes occurring at different moments in the two ears. In high frequency sounds where the wavelength is less than the distance between the ears several wave oscillations may occur, resulting in ambiguous phase comparisons. In addition, the nerve leading from the ear is unresponsive for about a thousandth of a second after each oscillation, so a sound with more than a thousand vibrations per second would not be completely represented by nerve impulses (Marler, 1959).

Accurate comparisons of differences in time of arrival of sound at the two ears is dependent on the way a sound begins and ends rather than on frequency ranges. It has been found that sharp discontinuities are most easily perceived, especially if frequently repeated (Marler, 1959).

Marler concludes that the ideal sound permitting source localization "will include a high pitch for location by intensity difference, a low pitch for location by phase difference, and it will be sharply broken and repetitive for location by time difference" (1959:175). In man it has been

found that pure tones in the region of 2.0 ~ 5.0 kHz are difficult to locate by comparisons of phase and intensity differences, being too high for the former and too low for the latter to be effective (Marler, 1955). For this frequency range only time differences can be used to successfully locate sounds. The lower limit of this frequency range is probably similar in the Sykes monkey due to the refractory period of the auditory nerve. However, the upper limit is probably higher (exactly how much so is yet to be determined) since the diameter of the Sykes' head is smaller than man's and the "shadowing effect" will thus not take place until a smaller wavelength or higher frequency is reached.

Five Sykes calls, about whose functions something is known, were chosen for investigation. These vocalizations will be examined in terms of whether they can or can not be easily localized by phase, intensity, or time differences. The five calls are the nyah, boom, chirp, squeal, and shriek.

It has been mentioned elsewhere that the nyah call given by adult males functions to promote group cohesion and coordinate group movements. Struhsaker (1970) emphasizes that by doing so, such calls may also serve to maintain reproductive isolation in areas of mixed species associations. When the call is given the group members, who have been dispersed at the time, begin to move in the direction from which the call came. The call is loud and carries over considerable distances. Visual contact does not seem to be of importance here so one would expect the nyah, in keeping with its function, to be a call which is easily localized. Analysis of its

structure shows this to be the case. The average range of major energy distribution for the nyah was shown to be between 0.82 and 5.46 kHz (Table 3) which would apparently include a low enough pitch for localization by phase differences. The upper limit of this range would appear at first glance to be too low to facilitate localization by intensity differences since it most likely falls within the "hard-to-locate" range discussed earlier. However, since in total energy distribution the upper frequencies of the nyah may extend to 16.0 kHz or more, localization by means of intensity differences is indeed possible. The call is of a short duration (0.31 seconds), has an abrupt beginning, and is almost always repeated thus enabling localization by temporal differences. In short, the nyah call fulfills all three of Marler's requirements for an ideal sound permitting source localization. Indeed, this is what one would expect of a call which apparently plays such a vital role in group maintenance and cohesion.

Another call whose function is apparently concerned with group cohesion without requiring visual contact with the caller is the boom vocalization. This call, however, differs from the nyah in several respects. The boom is a very low-pitched call with an average energy distribution of 0.01 - 0.40 kHz (Table 5). This low frequency would permit localization by phase differences but not by intensity differences. Although the call is of a short duration (0.20 seconds), it is not repeated, nor does it begin or end abruptly, thus making localization by temporal differences difficult. There are several possibilities which may account for the structure

of this call. Although the boom would not appear as ideal for localizing a sound source as the nyah, perhaps it is given under circumstances where an extreme degree of localization would be disadvantageous to the caller or the group, such as in reaction to the observer or a potential predator. Another possible explanation is that perhaps phase difference alone is an efficient means of sound localization as long as the call is restricted to very low frequencies. In addition, a low-pitched group cohesion call might be used because low frequency sounds carry over greater distances than sounds of higher frequencies (Moynihan, 1967). Also, there is less chance that a low-pitched call will be refracted by trees or other objects as is the case with high-pitched sounds (Marler, 1955), which is obviously an important consideration for an arboreal species. The key to explaining the nature of the boom clearly lies with a better understanding of its function as well as with the formulation of an experimental approach which would test the localization properties of the call.

The chirp acts as a threat/alarm call and its physical properties would seem to facilitate localization. Although the average major energy distribution of 2.91 - 6.14 kHz (Table 1) falls within the "hard-to-locate" zone, the total energy range of 0.10 - 16.0+ kHz most likely permits localization by means of phase and intensity differences. The call has an abrupt beginning, is of short duration (0.18 seconds), and is usually repeated. With increasing intensity or levels of excitement, the call is repeated more frequently and may have an even more abrupt beginning. Localization by

comparison of temporal differences is clearly possible and may be of considerable importance. One might expect an alarm call to be given in such a way as to prohibit localization of its source for safety's sake, as is the case for some avian calls (Marler, 1955). That this is not the case for the chirp is supported by the observation that the other group members look toward the caller upon hearing the chirp and may then chirp also. In addition, the caller is frequently exposed in the open when giving the call and may not move back into the brush for some time; in fact, other Sykes may actually move up to be near the caller as they join in chirping. Since the chirp is easily located it aids in indicating the source of danger to other group members and in enlisting their support in threat.

The last two calls to be considered are the squeal and shriek. Both seem to be associated with agonistic encounters although their exact function is undetermined. Their energy distributions of 3.30 - 7.87 kHz for the squeal (Table 6) and 3.20 - 8.74 kHz for the shriek (Table 7) are apparently within the "hard-to-locate" range. The calls are of a longer duration than the others which have been discussed, 0.63 seconds (squeal) and 1.01 seconds (shriek), and both start and end gradually. Precise localization of the sound source would appear to be difficult. However, the most important difference between the shriek and squeal and the other calls which have been described is that the functions of the latter require transmission over distances, whereas the shriek and squeal apparently function in close-range agonistic encounters.

Consequently, other channels of communication, such as facial expressions or touch, may contribute to the message content and indicate the location of the vocalizer.

It is difficult to explain the physical properties of the remaining calls in the Sykes' repertoire until more is known of their function. Since most of these calls seem to function on a close-range basis, one would expect other channels of communication to be of some importance in signal transmission.

It should be emphasized that a discussion of the structural and functional components of a call in terms of its localization properties is an oversimplification of the nature of primate vocalizations. Other factors, such as requirements for species specificity and individual identification or the nature of the physical and social environments, may affect the physical structure of a primate call. For example, Marler (1965) points out that in those calls used over distances to maintain spacing between groups, the requirements of species specificity necessitates use of a larger range of sound properties than in close-range communication. These spacing calls, says Marler, are therefore more highly structured and purer in tone. It is possible, therefore, that requirements for species specificity might be partly responsible for the highly structured nyah call of the Sykes monkey.

Oversimplified generalizations about primate vocalizations can be dangerous and misleading. A statement that arboreal species living under conditions of low visibility

have developed elaborate high-pitched calls (Cartlan and Brain, 1968) gives the misleading impression that a high pitch alone makes such calls functionally significant and fails to recognize and account for the existence of low-pitched calls among such species. What is needed instead is a structural-functional analysis to furnish clues as to why a particular structure or form may predominate. It is hoped that the analysis presented in this section has demonstrated the feasibility of such an approach.

Taxonomic Implications

The genus Cercopithecus is said to have more species and forms than any other primate genus in Africa (Struhsaker, 1970). Its species have usually been distinguished taxonomically on the basis of pelage coloration. Unfortunately, wide variability in pelage coloration within the genus and within its species has resulted in some disagreement over the interpretation of phylogenetic affinities. In cases where morphological characters are inadequate or equivocal, the taxonomist has been urged to make use of data from studies in behavior, ecology, physiology, and biochemistry (Lanyon, 1969).

Through the use of improved recording equipment and the development of the sound spectrograph, one aspect of behavior, i.e., vocal communication, has been shown to be of some significance in taxonomic studies of orthopteran insects (Alexander, 1962), anuran amphibians (Bogert, 1960; Blair, 1962, 1964), and birds (Marler, 1957; Lohrl, 1963). Studies

such as that of Struhsaker (1970) have indicated that vocalizations, when used with the same precautions and care applicable to any potential taxonomic character, can be of considerable importance in primate taxonomy as well. Struhsaker examined the taxonomic position of several Cercopithecus species, basing his decisions largely on similarities or differences in certain vocalizations.

One of the species studied by Struhsaker (1970) was Cercopithecus nictitans. Several authors have pointed out the strong physical resemblance between C. nictitans and C. mitis (Booth, 1956; Haddow, 1952; Kingdon, 1971; and Tappan, 1960). Hill (1966) placed C. nictitans in the mitis superspecies and the 1969 Wenner Gren Conference raised the question that perhaps C. nictitans and C. mitis might be best considered as conspecific (Thorington and Groves, 1970). A comparison of the vocalizations of these two species might shed some light on their phylogenetic relationship.

Of the two species, C. nictitans is the more restricted in distribution, being largely confined to the West African area. Two subspecies are generally recognized. C. n. martini is the most westerly located (Ghana, Nigeria, Cameroun). C. n. nictitans is also on the western coast (Gabon, Cameroun) but extends eastwards into the Central African Republic area. C. mitis, characterized by numerous subspecies, is much more extensive in its range, being found in central, east, and south Africa. C. mitis is said to be the only forest guenon having such a wide distribution in southern and eastern Africa (Kingdon, 1971). It apparently inhabited these areas

before climatic changes isolated many of the forests, thus closing them to those Cercopithecus species which have developed more recently (Kingdon, 1971). In fact, C. mitis is believed to be near the stock from which the main guenon radiation has derived (Kingdon, 1971). For a more detailed discussion of the distribution of the various C. mitis subspecies, the reader is referred to Rahm (1970).

The subspecies which will serve as the basis for the present discussion of vocalizations are C. n. martini and C. n. nictitans studied by Struhsaker (1970) in Cameroun and C. m. kibonotensis from the southeast Kenya coast whose vocalizations have been described in this paper.

The reader should note that the C. mitis and C. nictitans populations here being considered are allopatric, a situation which can make for considerable difficulty in assessing phylogenetic relationships (Mayr, 1969). In this regard, it is the examination of sympatric species which is most conclusive, since any mechanisms assuring species identity through reproductive isolation can be more reliably recognized in the sympatric state. However, Struhsaker (1970) has shown that interpopulation variability in the basic structure of vocalizations within a species appears to be minimal. The species he considered included C. aethiops (populations from East and West Africa), C. mona, C. nictitans (populations from both subspecies), and C. pogonias (populations from the subspecies pogonias and gravi). Within each of these species and across subspecies lines Struhsaker found that the vocalizations showed a considerable amount of

stability and uniformity. Therefore, it will be assumed that the vocalizations of C. mitis are relatively uniform throughout its range also. In this way, it will be assumed that the vocalizations of C. mitis kibonotensis of East Africa would be basically similar to those C. m. stuhlmanni and C. m. maesi, two western subspecies of C. mitis which are reported to be sympatric with C. n. nictitans at the eastern limits of its range (Rahm, 1970; Kingdon, 1971). Ideally, a study to determine whether C. nictitans and C. mitis are conspecific should be carried out in this area of sympatry. Until such studies are available, however, and until studies indicative of the extent of variation of the vocalizations within C. mitis are carried out, the investigation presented here will proceed on the assumption which has been made based on Struhsaker's analysis (1970). No attempt is being made, therefore, to present the findings of this study as a final taxonomic statement.

Hill (1966) apparently feels there is enough distinction between the western and eastern subspecies of the C. mitis group to warrant their separation into two different species, C. mitis and C. albogularis respectively. However, other workers (Rahm, 1970; Kuhn, 1967; Kingdon, 1971) have classified these as a single polytypic species. That hybrids have been reported between C. m. stuhlmanni and C. m. albogularis (Booth, 1968) not only tends to support the latter approach but also adds more weight to the assumption that isolating mechanisms, including any vocalizations which may function as isolating mechanisms, are probably uniform.

throughout the range of C. mitis. It should be pointed out that since the eastern subspecies of C. mitis are relatively isolated from other forest guenons while those in the west may be sympatric with several, such as, C. mona, C. ascanius, C. l'hoesti, and C. neglectus, there may be selective pressures operating in the west which may not be operating in the east. These differences may be reflected in the vocalizations of these species.

Struhsaker (1970) believes that the loud calls given by adult male Cercopithecus monkeys function to maintain reproductive isolation between species by enhancing group coherency, especially in response to alarming stimuli. In the sympatric state, therefore, the loud calls of two species would be different; Struhsaker, working with several species, found this to be the case.

A comparison of the loud calls which Struhsaker reports for C. nictitans (1970:407, 427) with those reported here for C. m. kibonotensis (Figs. 6-8 and Tables 3&4) reveals some differences. The nyahs of C. mitis cover a higher frequency range than do the pows of C. nictitans and have a more elaborate development of harmonics. The tonality of the C. mitis calls also has an arching configuration, rising and then falling in frequency, as opposed to the descending quality of the tonality in C. nictitans. The short nyahs have some spectrographic resemblance to the hacks of C. nictitans, but again a higher frequency is reached in C. mitis. No calls equivalent to the pow-hacks which Struhsaker found to be intermediate between pows and hacks were found for

C. mitis. Struhsaker could not discern any significant difference in the loud calls of the two subspecies of C. nictitans, nor could he distinguish the hacks of C. erythrotis and C. cephush (1970:408, 429) which he subsequently placed in a single species. The loud calls of C. mitis and C. nictitans are apparently not as similar as those of these other conspecific populations.

In addition, booms were recorded for C. mitis but not for C. nictitans and in this regard C. mitis resembles the mona superspecies. The C. mitis booms (Fig. 9 and Table 5) resemble the C. mona calls (Struhsaker, 1970:409, 431) very closely. However, since this type of call is restricted to such low frequencies, variability may be expected to be limited so that similarities may not be significant. Booms are typically given before a series of hacks in C. mona. Booms were also frequently heard in conjunction with nyah calls in C. mitis. However, these similarities in boom calls should not be taken to indicate an especially close relationship between C. mona and C. mitis. The hacks of C. mona (1970:410, 423) do not appear to be any more similar to those of C. mitis than the latter was to C. nictitans. In addition, only hack-type units were recorded for C. mona whereas C. mitis definitely shows two types, i.e., nyahs and short nyahs. No calls similar to the "ooo" contact calls reported by Struhsaker for the mona superspecies were found in C. mitis. There are also several differences between other calls of C. mona and C. mitis and these will be discussed below.

The chirp (alarm) calls of C. mitis (Figs. 1-5 and Tables 1&2) bear some resemblance to the chirps of C. nictitans and C. erythrotis-cephus (Struhsaker, 1970:411, 414, 435, 436). In terms of the spectrographic form of the chirps the three species are very similar, but those of C. mitis are of somewhat higher frequencies as well as of longer duration. Multi-unit chirps were present in all three species. Struhsaker (1970) found the chirps of C. erythrotis and C. cephus to be very similar. Some of these chirps were identical to those given by C. nictitans. Similarity in alarm calls among sympatric species faced with common predators may be explained as a case of parallelism. Struhsaker (1970) points out, however, that C. mona and C. pogonias also associate freely with C. nictitans and C. erythrotis-cephus but maintain very distinct alarm calls. Therefore, Struhsaker concludes that C. nictitans and C. erythrotis-cephus may be more closely related to each other than to C. mona.

Struhsaker (1970) reported grunts and chutters for C. nictitans and C. erythrotis-cephus but found that no such calls were given by members of the mona superspecies. The grunts are thought to function in maintaining group cohesion while the chutters were given during agonistic encounters. C. mitis has vocalizations similar to these grunts and chutters, although the samples for C. mitis are too small to be conclusive. A low, short chutter given by C. mitis (Fig. 15 and Table 10) resembles very closely the C. nictitans chutters described by Struhsaker (1970:419, 441) both in energy distribution and duration. However, the relationship of this

chutter to others of higher frequencies which have been reported for C. mitis in this paper is not clear. Struhsaker does not mention any other chutter types for C. nictitans and C. erythrotis-cephus but his 1970 study was apparently not intended to be descriptive of the complete sound repertoires. Therefore, it remains to be seen whether the existence of these other chutter-types in C. mitis is indicative of a significant species difference. The "err" reported here for C. mitis (Fig. 21 and Table 13) may be equivalent to the grunts; if so, some differences are apparent. While all the C. nictitans grunts (Struhsaker, 1970:418, 441) were single-unit phrases and the C. erythrotis grunts (Struhsaker, 1970: 418, 441) were either single- or triple-unit phrases, the "err" of C. mitis was made up of four or five units. Although unit and phrase duration for all three species are basically similar, the C. mitis call extends to a much higher frequency. Again, Struhsaker found that the grunts and chutters of C. erythrotis and C. cephush were very similar to each other and also to those of C. nictitans; the grunts, in fact, were indistinguishable.

Of the vocalizations discussed above, the one which plays the most important role in helping to maintain species identity through reproductive isolation is the loud call. Struhsaker points out that vocalizations having different functions evolve at different rates: "Calls serving to alarm or coordinate groups may evolve more slowly than those enhancing reproductive isolation through the maintenance of conspecific intragroup cohesion around one male" (1970:370). If

this assumption is correct, then one would expect the chirps, grunts, and chutters to not be under the same pressures for species specificity that influence the loud calls. Furthermore, species showing similarities in these calls may be more closely related to each other than to species which do not have such similar calls (Struhsaker, 1970).

It has been shown that the loud calls of C. mitis are readily distinguishable spectrographically from those of C. nictitans. Since these differences are greater than those found among conspecifics, a separate specific status for C. mitis and C. nictitans seems warranted at this time. This conclusion is further supported by the observation that the chirps, grunts, and chutters of C. mitis are also not as similar to those of C. nictitans as are these calls within the C. nictitans subspecies and within the C. erythrotis-cephus species. According to Struhsaker (1970), the fact that grunts, chutters, and chirps are absent in the mona superspecies would seem to indicate that these calls are not to be interpreted as conservative, widespread vocalizations but rather may be indicative of close phylogenetic relationships. Following Struhsaker's reasoning, one can conclude that the similarities of the C. mitis calls to those of C. nictitans and C. erythrotis-cephus, while not indicative of conspecific status, would indicate that C. mitis, C. nictitans, and C. erythrotis-cephus are more closely related to each other than to the mona superspecies.

It should be emphasized again that future studies may reveal that the vocalizations of the more westerly

distributed C. mitis populations may be considerably different from those reported here for C. m. kibonotensis. Information as to the amount of variation in vocalizations throughout C. mitis' range is needed to either support or refute the assumption made here concerning their supposed stability and uniformity. Information is also needed as to the extent to which C. mitis and C. nictitans may associate in their zones of sympatry. If the two species should be found to hybridize freely in these zones, then serious consideration of a conspecific status would be called for.

Although the samples collected for C. mitis were often too small to permit rigorous statistical comparison and testing, it is recognized here that a true assessment of the degree of relationship between two species must be based on careful statistical measures before any great reliability in the data may be assumed. It is also recognized that taxonomic conclusions should not be based on one or a few characters alone, but should depend instead on the total assessment of morphology, physiology, behavior, karyotypes, etc. However, if Struhsaker's observation is true that "of all the single classes of characters so far used, vocalizations seem the most stable and thus the single most reliable indicator of phylogenetic affinities within this genus" (1970:402), then future studies of vocalizations of the Cercopithecus species may very well prove to be of considerable importance in the assessment of phylogenetic relationships within this highly variable genus. The analysis of vocalizations, therefore, should merit considerable attention by primate taxonomists.

CHAPTER III

VOCALIZATIONS OF THE COLOBUS MONKEY

In sharp contrast to the relatively vocal Sykes monkeys are the taciturn colobus monkeys (Colobus polykomos palliatus). These beautiful, black and white primates sit for hours at a time without making a sound.

Colobus live in small groups; those in the study area ranged in size from three to eight animals per group. They maintain a relatively small territory in comparison to the Sykes. Each troop was observed to occupy the same general area for the duration of the study and, as a result, they could be located quite readily.

The taxonomic designation, C. polykomos, being used here follows that of Schouteden (1947), Tappen (1960), Napier and Napier (1967), and Kuhn (1967). However, others, i.e., Schwarz (1929), Dandelot (1968), and Rahm (1970), differentiate C. angolensis from C. polykomos and under this system the colobus of this study would fall within the former designation. It is generally agreed that before the taxonomic problems can be resolved more information is needed about the adaptations of these monkeys and areas of distribution overlap need to be investigated (Tappen, 1960).

The colobus have one habit which, while not vocal, definitely serves as a means of communication. The colobus take fantastic leaps, land with a resounding thump against tree limbs and branches, and continue in this way jumping from tree to tree. The other colobus are alerted (probably by both the sight and the sound) and look in its direction, watching the leaping colobus closely. These displays are quite impressive and seemed to be given in response to the observer's presence, probably functioning in part as an attempt to intimidate the intruder.

This ability to take leaps of considerable distance also serves to indicate danger and the direction of troop movement. If a colobus is startled, it will vault itself seemingly into midair only to come crashing down into the thicker brush below. The other colobus are immediately alerted and also leap down into the lower level. A similar observation has been made by Schenkel and Schenkel-Hulliger (1967). In a short while, when the danger has apparently passed, the colobus will gradually move back up into the higher branches. Marler (1968) also emphasizes the reliance of the colobus on visual cues for maintaining intragroup spacing during movement, pointing out that the conspicuous color of the colobus and their habit of keeping high in the trees facilitate visual coordination of their activities.

Colobus tend to remain silent unless sufficiently disturbed. Such disturbing circumstances included the close proximity of the observer, the milling around of a group of four or five dogs in the woods directly below the colobus

troop, and the circling overhead of a pair of Bateleur Eagles (Terathopius ecaudatus).

On the latter occasion, a group of eight colobus were sitting relaxed in the tall trees. In this troop was a female with a small white infant. The female had been sitting unperturbed with the infant squirming about in her lap but as a pair of Bateleur Eagles slowly circled closer she became quite tense and attentive, craning her neck to watch the birds. After a few moments she clutched the infant to her and moved over to a more thickly leaved tree. As she did so, a male colobus gave a croaking, snorting sound and bounded over to the female's side, also watching the eagles intently. Moments later, the male was observed holding the infant so he must have taken it from the female when he moved near her. However, incidents such as this were infrequent and other than the vocalizations of infants or juveniles, the troop was generally silent.

The white infant was a focal point of interest for the entire group. In fact, all the adult females were so interested in the infant that at times it was very difficult to determine who the actual mother was. This was further complicated by the frequent practice of passing the infant from one adult to another when it would begin to squirm and squeal.

The colobus were frequently found in the same immediate vicinity with the Sykes monkeys. The two species could often be seen feeding in the same trees or even on the same branch just a few feet apart.

Classification of Calls

Snort

A loud, snort-like sound (Figs. 23&24 and Table 15) was given by adult colobus on several occasions. The call is most likely an alarm and/or threat call as it was evoked by the sudden appearance of the observer, by a group of dogs, and by the Bateleur Eagles. A similar call was reported for C. polykomos by Hill and Booth who described it as an "explosive snort, uttered partly through the nose" which was given by adults of both sexes (1957:311).

TABLE 15

SNORT

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	4/3	1.33	1.00-2.00
Unit Duration (secs.)	4	0.13	0.06-0.15
Lower Limit of Major Energy (kHz)	4	0.25	0.25-0.25
Upper Limit of Major Energy (kHz)	4	10.45	3.30-13.00

The snort begins abruptly and appears primarily as a nontonal vocalization on the sonogram. The call averages approximately 0.13 seconds in length (N=4). The major energy distribution is about 0.25 - 13.00 kHz with the greatest concentration of noise showing on the sonogram in the vicinity of

4.0 - 8.0 kHz. The snort usually consisted of a single-unit phrase, although on one occasion a two-unit snort phrase was given, the two units being separated by an interval of 0.44 seconds. The second snort was approximately only half as long as the first and its energy distribution was confined to a lower frequency range (0.25 - 3.30 kHz).

Snort-Croak

The snort may stand by itself as a call or it may precede another call identified here as the snort-croak (Figs. 25-27 and Table 16). Marler (1970) mentions that C. gueraza has a distinctive roaring call which sometimes may be preceded by a snort. This may be equivalent to the snort-croak described here, but this writer hesitates to use the term 'roar' because such a term would seem to imply a single, long, loud call which definitely was not the case in the snort-croak. The snort-croak is probably equivalent to the "full call" reported by Hill and Booth (1957) as given by adult male C. polykomos. These authors also noted that the snort-like alarm call may precede the full call.

A jumping-roaring display said to be highly ritualized and which may function as a mechanism of intergroup spacing has been described by Ullrich (1951) and Schenkel and Schenkel-Hulliger (1967). The roaring is reported to spread from group to group so that a chorus develops. Although the snort-croak was never heard under these circumstances while this observer was in the field, it is possible that it is equivalent to this roaring display. Likewise, whether the "full call" described by Hill and Booth (1957) is the same as the roaring display

can not be determined from their report. Based on the verbal descriptions of the calls, they all seem to be similar; confirmation of this must await spectrographic comparison.

The snort-croak is actually a long bout consisting of three different phrase-types. Besides the initial single-unit snort phrase, the snort-croak includes a multi-unit phrase of a croaking, gutteral sound given in alternation with a faint, short, inhalation, single-unit phrase.

The initial snort of the snort-croak is very similar acoustically and spectrographically to the snort phrase which has already been described. The phrase duration of the snorts of the snort-croak averages 0.11 seconds and the major energy is distributed over a range of 0.25 - 12.50 kHz (N=4).

Each croak phrase is composed of several short tonal units. Those measured had anywhere from eight to sixteen units (mean of 10.21 units; N=24). Each unit is of a very short duration (0.01 or 0.02 seconds) but together as a phrase the mean duration is 0.24 seconds (N=24). The croak is low in frequency and has a deep, gutteral sound. The average distribution of the heaviest concentration of energy is from 0.26 - 0.97 kHz. The number of croak phrases per bout is variable, averaging 5.38 phrases per bout (N=13) but ranging from two to seventeen. It should be pointed out that the seventeen croak phrases represent an extreme; the next highest number of phrases is nine. The bout with seventeen phrases was given during the encounter with the eagles and was given more rapidly than the others. In addition, the croak phrases were shorter, averaging 0.16 seconds as compared to an average

of 0.34 seconds (N=11) for the other croak phrases. A portion of this seventeen-phrase bout is pictured in Figure 27.

In between the croak phrases is a faint sound made as the colobus inhales. This unit is nontonal and averages 0.05 seconds in duration (N=22). The average major energy distribution of this single-unit phrase is 0.27 - 1.25 kHz (N=22).

TABLE 16

SNORT-CROAK

	Number (N)	Mean (\bar{x})	Range (R)
<u>Snort Phrase</u>			
Units/Phrase	4/4	1.00	1.00-1.00
Phrase Duration (secs.)	4	0.11	0.10-0.12
Lower Limit of Major Energy (kHz)	4	0.25	0.25-0.25
Upper Limit of Major Energy (kHz)	1	12.50	12.50-12.50
<u>Croak Phrase</u>			
Units/Phrase	245/24	10.21	8.00-16.00
Unit Duration (secs.)	245	0.01	0.01-0.02
Interval Between Units (secs.)	221	0.01	0.01-0.02
Phrase Duration (secs.)	24	0.24	0.15-0.43
Lower Limit of Energy (kHz)	24	0.26	0.25-0.40
Upper Limit of Energy (kHz)	24	0.97	0.75-1.00

TABLE 16 (Continued)

	Number (N)	Mean (\bar{x})	Range (R)
<u>Inhalation Phrase</u>			
Units/Phrase	22/22	1.00	1.00-1.00
Phrase Duration (secs.)	22	0.05	0.04-0.07
Lower Limit of Major Energy (kHz)	22	0.27	0.25-0.40
Upper Limit of Major Energy (kHz)	22	1.25	0.70-2.00

Gecker - White Infant

The gecker (Fig. 28 and Table 17) is a high-pitched, squeaky sound and was given quite frequently by a white infant colobus. Usually the infant would be squirming and wriggling around while giving the call but it was impossible to tell if it was trying to nurse. The adult holding the infant would either shift it in its arms or else let another colobus take it.

The frequent, at times almost constant, geckering by the infant was in sharp contrast to the usual nonvocal attitude of the rest of the troop. As a result, the somewhat noisy infant seemed to be able to solicit attention and be an important focal point for the rest of the group.

Energy distribution of the gecker ranged from 0.25 to 13.00 kHz, but on the sonogram the darkest portion averaged

3.64 - 6.69 kHz (N=11). The mean phrase duration was 0.32 seconds (N=11) and several such single-unit phrases were combined to give bouts of variable length. It is difficult to assess the duration of a bout or the number of phrases per bout since the call varies throughout in loudness and gives an impression of randomness and irregularity rather than of a fixed pattern of phrase sequences.

TABLE 17
GECKER - WHITE INFANT

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	11/11	1.00	1.00-1.00
Phrase Duration (secs.)	11	0.32	0.27-0.40
Interval Between Phrases (secs.)	9	0.13	0.05-0.28
Lower Limit of Major Energy (kHz)	11	3.64	2.00-4.50
Upper Limit of Major Energy (kHz)	11	6.69	6.10-7.70

The gecker is both tonal and nontonal, with the tonal section first forming an arch-like pattern on the sonogram which then levels out into the noise component. As mentioned above, one of these "arches" is considerably darker than the rest; the others occur above and below it in a harmonic pattern.

Err - White Infant

On one occasion a phrase consisting of three "err" sounds was heard at the end of a geckering sequence (Fig. 29 and Table 18). The exact relationship of this call to the gecker is not understood; it may be a part of the gecker or it may be an individual vocalization. However, on the sonogram the call is different in appearance from the gecker.

TABLE 18
ERR - WHITE INFANT

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	3/1	3.00	3.00-3.00
Unit Duration (secs.)	3	0.11	0.03-0.15
Interval Between Units (secs.)	2	0.05	0.05-0.05
Phrase Duration (secs.)	1	0.35	0.35-0.35
Lower Limit of Energy (kHz)	3	0.63	0.50-0.90
Upper Limit of Energy (kHz)	3	2.13	1.80-2.50

The mean duration of the three tonal units was short at 0.11 seconds (N=3). The "err" was lower in pitch than the gecker, with a mean energy range from 0.63 to 2.13 kHz (N=3). The duration of the phrase as a whole was 0.35 seconds.

Gecker - Juvenile

A call similar acoustically and spectrographically to the gecker of the white infant was given by a juvenile (Fig. 30 and Table 19). This individual had already attained its black and white coloration and, except for its smaller size, it was indistinguishable from the adult colobus. The juvenile no longer seemed to be very dependent on its mother although it was carried occasionally, apparently when frightened by the observer.

The juvenile gecker is also composed of tonal arch-like bands passing into nontonal components. Harmonics are present but the bands are closer together and more numerous than in the infant gecker.

TABLE 19
GECKER - JUVENILE

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	13/13	1.00	1.00-1.00
Phrase Duration (secs.)	13	0.11	0.04-0.14
Interval Between Phrases (secs.)	11	0.02	0.01-0.05
Lower Limit of Major Energy (kHz)	13	2.60	1.90-3.80
Upper Limit of Major Energy (kHz)	13	8.05	6.00-10.10

The individual single-unit phrases were of shorter duration than those given by the white infant, with an average length of 0.11 seconds (N=13). The average energy distribution ranged from 2.60 to 8.05 kHz (N=13), but again one band was somewhat darker than the rest at approximately 4.0 - 5.0 kHz. As in the infant gecker, it is very difficult to judge the duration of a bout or to determine the number of phrases per bout.

Occurring in the geckering bout on one occasion was a phrase which appeared on the sonogram as a single, wavy, linear unit, 0.54 seconds in duration (Fig. 31). The unit is basically tonal and occupies a frequency range of approximately 2.90 - 6.00 kHz. The darkest portion was again in the vicinity of 4.0 - 5.0 kHz so perhaps this phrase is but a series of geckering phrases given close together and lacking harmonic development.

The gecker was given by the juvenile as it was startled by the observer and ran to an adult female. Upon being embraced by the female, the juvenile stopped vocalizing.

CHAPTER IV

VOCALIZATIONS OF THE BABOON

Vocalizations and Crop-Raiding

The information collected on the baboon vocalizations formed part of a larger study on baboon crop-raiding behavior. Unfortunately, conditions were somewhat less than ideal at the Shimoni site during the time this observer was in the field. This site promised to be the best suited for making recordings and observing the baboons' behavior. However, due to seasonal conditions and a long drought in the area, no significant crops were being grown other than a few remnants gone to seed from the last growing season. In addition, the Africans who usually sit up in observation platforms in order to spot baboons and chase them from the field were not present.

When in the area a few years earlier, Maples (personal communication) noted what, superficially at least, appeared to be diversionary behavior. It seemed that one group of baboons would vocalize and thus attract and keep the attention of the shamba, or farm, guards while the rest of the troop would silently move into the farm a short distance away and raid the crops growing there. If this behavior were indeed coordinated and intentional, it would shed an interesting and new light on the nature of communication

systems among nonhuman primates. It was the purpose of this part of the study to investigate and record those vocalizations given in conjunction with this behavior.

Although the normal raiding conditions were absent during the course of this observer's investigations, the baboons did come to the shamba practically every day to forage for whatever remains could be found in the field. As a result, enough information was collected to allow at least a tentative explanation as to the nature of this seemingly deliberate "decoy" behavior.

Although shamba guards were lacking and consequently the raiding situation not as tense as it might have been under normal circumstances, it was noted that the baboons, in reaction to an observer moving about rapidly in the field, would move into the forest edge and gradually begin to move silently around the perimeter of the farm. The baboons at the rear of this troop movement would be up in the trees giving the threat/alarm bark. It is to these vocalizing baboons that the observer's attention is drawn. Consequently, he remains nearer to this group of baboons and, presumably, the shamba guards would be inclined to do the same. The vocalizing animals tend to minimize their own exposure to danger by sounding the alarm when the human intruder is moving away or looking in another direction, a practical behavioral adaptation since shamba guards may be armed with rocks, sticks, or bows and arrows. With the humans' attention thus drawn to this vocalizing group, the rest of the troop is relatively free of human intervention and has the opportunity to enter the shamba again to carry out additional raids.

It would seem, therefore, that even though the vocalizations given during the raids are diversionary in nature, they are probably not deliberately intended to be so. Instead, the calls given in reaction to the intruding human help to set up a fortuitous chain of events which allows part of the troop to continue raiding.

At Roka, similar observations were made although the conditions were somewhat different. Instead of a farm surrounded on three sides by forest, as was the case at Shimoni, the farms at Roka were separated from the forest by a fairly well-traveled road. When raiding, the baboons would have to come out of the forest and cross the road to enter the farms. Unlike Shimoni, crops were being grown in most of the fields and some farms were protected by shamba guards, usually women or children. In general, these baboons were not very vocal at all but would carry out their raids in silence. But again, it was observed that vocalizations of any kind or any movement in the trees would tend to attract the guards to that area while further down the road other baboons would be free to enter the farms undisturbed. Although not intentional, such behavior functions very well as a decoy mechanism.

The calls described in the following sections were recorded during encounters such as those described above.

Classification of Calls

Two-Phase Bark

The two-phase bark (Figs. 32&33 and Table 20) was recorded on one occasion at Roka. This was just after a shamba

raid had been completed and all the baboons were on the forest side of the road. The observation vehicle was driven adjacent to the point of entry into the forest. It was then that a large, fully adult male conspicuously sitting in a tall tree at the forest edge emitted two two-phase barks. The two-phase bark has been reported by Hall and DeVore (1965) as an attack/threat vocalization given in reaction to humans and large predators.

TABLE 20
TWO-PHASE BARK

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	2/2	1.00	1.00-1.00
Phrase Duration (secs.)	2	0.62	0.51-0.73
Lower Limit of Energy (kHz)	2	0.25	0.25-0.25
Upper Limit of Energy (kHz)	2	4.10	3.20-5.00

The two-phase bark is a loud, tonal, single-unit phrase of low frequency and long duration. The energy distribution for the first two-phase bark is from 0.25 to 5.00 kHz and the distribution for the second is 0.25 - 3.20 kHz. However, the heaviest concentration of energy for both calls is in the 0.50 - 1.50 kHz range. The duration of the calls is 0.73 seconds for the first and 0.51 seconds for the second.

On the sonogram the call appears as a very dark band in the lower frequencies with some harmonic development.

Bark

Humans moving about in the farm at Shimozi would usually provoke bark-like vocalizations (Figs. 34&35 and Table 21) from nearby baboons who would then withdraw into the forest.

There seemed to be two types of barks distinguishable both acoustically and spectrographically; however, this may be due to sex and/or age differences. Basically, the difference seems to be one of pitch, with one bark type noticeably lower and less intense. Both may be described as single-unit phrases.

TABLE 21

BARK

	Number (N)	Mean (\bar{x})	Range (R)
<u>Bark I</u>			
Units/Phrase	12/12	1.00	1.00-1.00
Phrase Duration (secs.)	12	0.32	0.20-0.40
Lower Limit of Energy (kHz)	12	0.27	0.25-0.50
Upper Limit of Energy (kHz)	12	4.13	3.70-5.00
<u>Bark II</u>			
Units/Phrase	7/7	1.00	1.00-1.00
Phrase Duration (secs.)	6	0.32	0.25-0.45

TABLE 21 (Continued)

	Number (N)	Mean (\bar{x})	Range (R)
Lower Limit of Energy (kHz)	7	0.48	0.40-0.70
Upper Limit of Energy (kHz)	7	2.88	2.50-3.00

The average energy distribution for Bark I is 0.27 - 4.13 kHz (N=12). The call is tonal and harmonics are well developed. The mean duration is 0.32 seconds (N=12).

Bark II is lower in pitch with an average energy distribution of 0.48 - 2.88 kHz (N=7). The harmonic pattern does not seem to be as well developed here as in Bark I and the upper frequencies of the call are somewhat weaker. The call averages 0.32 seconds in length (N=6).

Yak

The yak (Fig. 35 and Table 22) was believed to have been given by a juvenile. It was given under the same conditions as the barks and was given in conjunction with them.

Structurally the yak is very similar to the barks (especially Bark I) on the sonogram. It too consists of a single-unit phrase. The main difference is that the yak is higher in pitch and has a very well-developed harmonic pattern. The yak is also acoustically distinguishable from the barks.

TABLE 22

YAK

	Number (N)	Mean (\bar{x})	Range (R)
Units/Phrase	3/3	1.00	1.00-1.00
Phrase Duration (secs.)	2	0.30	0.30-0.31
Lower Limit of Energy (kHz)	3	0.50	0.50-0.50
Upper Limit of Energy (kHz)	3	6.40	5.00-8.0+

The average energy distribution of the yak is approximately 0.50 - 6.40 kHz (N=3); however, the harmonic pattern on one occasion extended beyond 8.0 kHz. The average duration of the call is 0.30 seconds (N=2).

On the occasion when the calls were recorded the yak occurred in a repeated sequence of Bark I, Yak, Bark II given while an observer moved about in the shamba at Shimoni. The baboons giving the calls were at the forest edge. While they were vocalizing, the rest of the troop was quietly circling the farm a short distance within the forest.

CHAPTER V

SUMMARY AND CONCLUSIONS

The study of primate behavior developed rapidly in the years following World War II to become a popular discipline within the fields of zoology and physical anthropology. However, one aspect of its study, primate communication, has only recently begun to receive the attention which it rightly deserves. That as yet no single study has been able to deal with social communication in all its aspects is testimony to the complexity of the task. Instead, individual researchers have chosen to study some specific aspect or channel of communication, usually of a single species, in the hope that with enough information collected in this manner a larger, more comprehensive overview of the communication process as a whole may eventually be possible. It is with this intent that the present study has been conducted.

By means of sonograms the vocalizations of three species of Old World monkeys (Sykes monkey, colobus monkey, and baboon) were illustrated, described, and analyzed. The conclusions and findings are summarized in the following sections.

The Sykes Study

1) Fourteen Sykes vocalizations were catalogued and described in terms of their physical characteristics (frequency, duration, tonality, etc.). The possible functional significance of the calls and any accompanying behavior was also presented.

2) The vocalizations were examined in terms of discreteness vs. gradedness. Most of the calls were found to be of the discrete type but calls forming a possible gradient were also discussed. It was emphasized that demonstrating the existence of graded signals does not imply the existence of a graded communication system.

3) The Sykes vocalizations show considerable variety in pitch or frequency and timing. An attempt was made to correlate these differences in structure with differences in functional requirements, particularly the need for localization. It was found that the properties of calls concerned with group cohesion and alarm or threat which were transmitted over distances without necessarily the aid of visual contact were such as to facilitate localization of the vocalizer. On the other hand, the structure of calls which were transmitted at close-range where visual or other cues may be operable did not show those features which would facilitate localization.

4) The taxonomic position of the Sykes monkey, Cercopithecus mitis, in relation to C. nictitans has been a matter of some speculation. A preliminary analysis and

comparison of the vocalizations of the two species indicated that separate specific status should be maintained at this time. However, analysis revealed that C. mitis was more closely related to C. nictitans and C. erythrotis-cephus than to the mona superspecies.

The Colobus Study

- 1) Two calls were described for adult colobus as well as one for juveniles and two for infants. When possible, their probable functions were discussed and any accompanying behavior was described.
- 2) Although vocalizations were the primary concern in this study, a nonvocal communication pattern, the jumping display, seemed to play an important role in the life of the relatively nonvocal colobus. This behavior was described and its possible functional significance was discussed.

The Baboon Study

- 1) The physical characteristics of four types of calls given during crop-raiding were described.
- 2) The apparent "decoy" effect of the calls in attracting the attention of farm guards protecting the crops while other baboons silently entered the fields to raid was described and analyzed. It was concluded that the calls were fortuitously diversionary in nature rather than representing a deliberate and intentional plan of behavior.

There had been a tendency in studies of primate behavior and communication to accept as generalizations for all species that which had been described for but a few well-studied populations. That the behavior of all species can not be seen in a baboon-rhesus context or that the behavior of all baboons is not typified by the Nairobi Park population, for example, has become increasingly apparent as more and more primate species and populations in various ecological settings are being studied.

Before the formation of encompassing generalizations then, if indeed such should prove to be possible, the primary need in communication studies is one of collection of data on as many species as possible. Ideally, information on communication systems should be accompanied by information on behavioral context and functional significance. Through observation of the behavioral context accompanying a communicatory act, something can be learned regarding the functional significance of a particular vocalization, facial expression, etc. Analysis of the relationship between structure and function may indicate why certain structural traits have proved adaptive and have been maintained through the process of natural selection. Comparison of such findings from several studies on separate species or on different populations of the same species may reveal ways in which the ecological setting can influence which adaptive mechanisms will predominate. In addition, an understanding of the degree of variation to be found in communication patterns within species will aid in taxonomic interpretations and in the assessment

of vocalizations and other channels of communication as taxonomic characters. In this way, one can begin to understand something of the relationship between communication, organized social life, and ecology of man's closest relatives, the nonhuman primates.

Finally, it should be emphasized that primate communication should not be studied solely in terms of how many features of human language may or may not be present, but also as an entity worthy of study in its own right. However, an understanding of the nature of communication systems among nonhuman primates and how these systems relate to social organization and environment may eventually shed light on the circumstances accompanying the origin of language in man and on the nature of this early system.

That primate communication is a behavior which has proved adaptive and evolutionarily successful can not be disputed, but the mechanisms behind that adaptation are as yet not fully understood. It is hoped that through further study and fieldwork more and more information may be collected and correlated to reveal something of the adaptive significance of communication systems in general and of how these systems are integrated into the larger whole of primate social life. It is this intricate weaving and integration of behavioral systems, of which communication is but one, which makes the coordination of individuals into a society possible, and which in turn insures the survival of the species.

PLATES

SYKES MONKEY

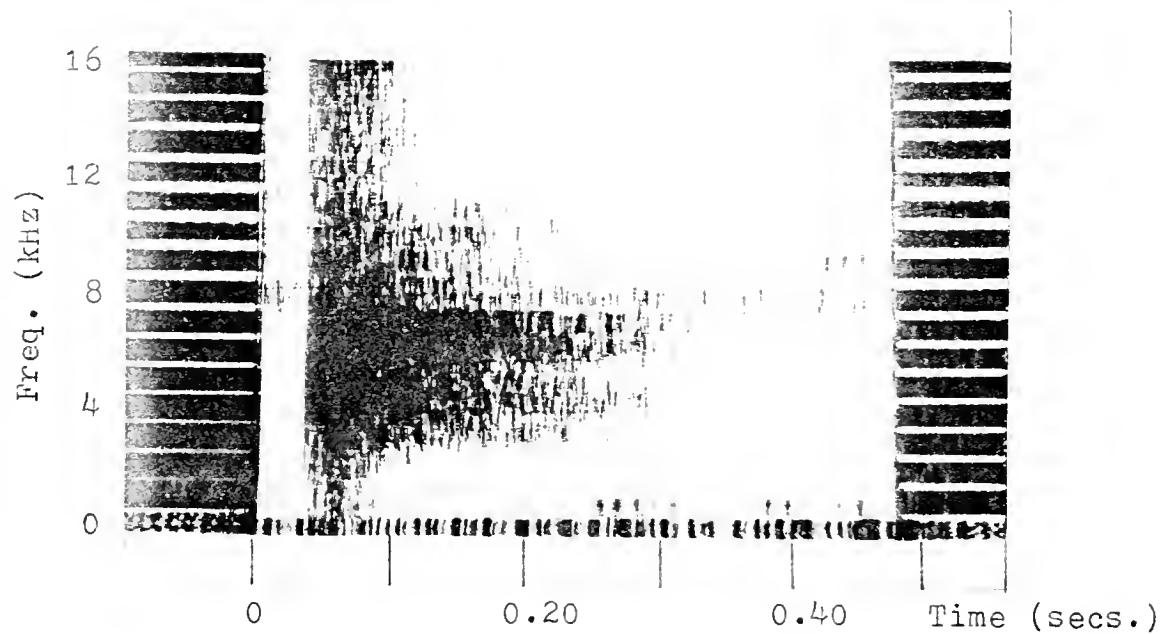


Figure 1. Chirp

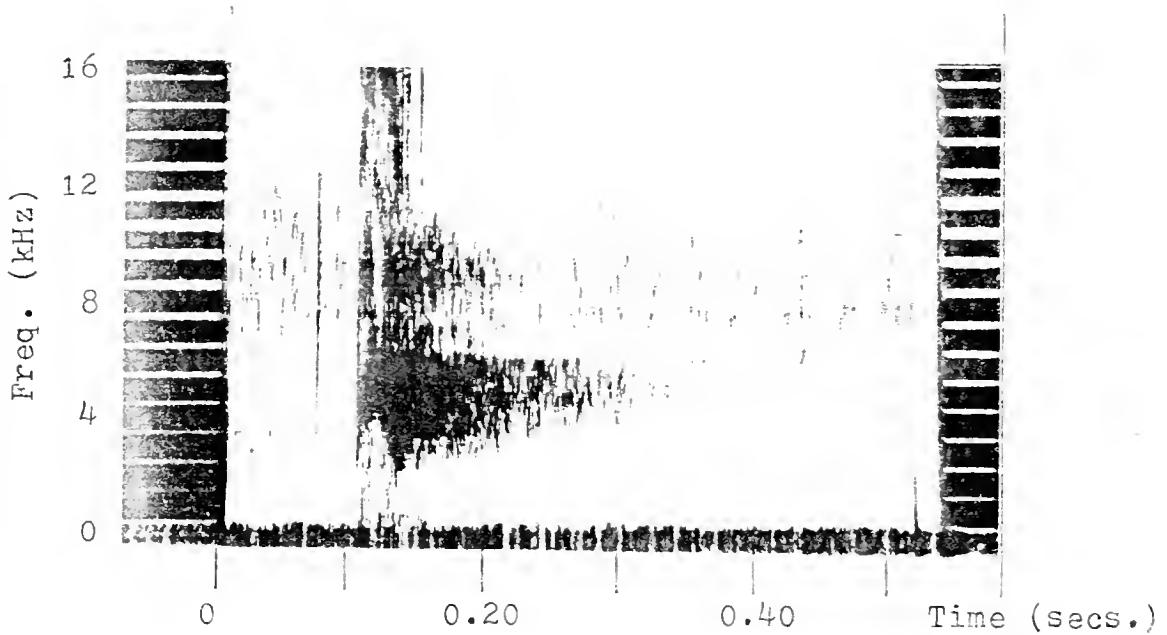


Figure 2. Chirp

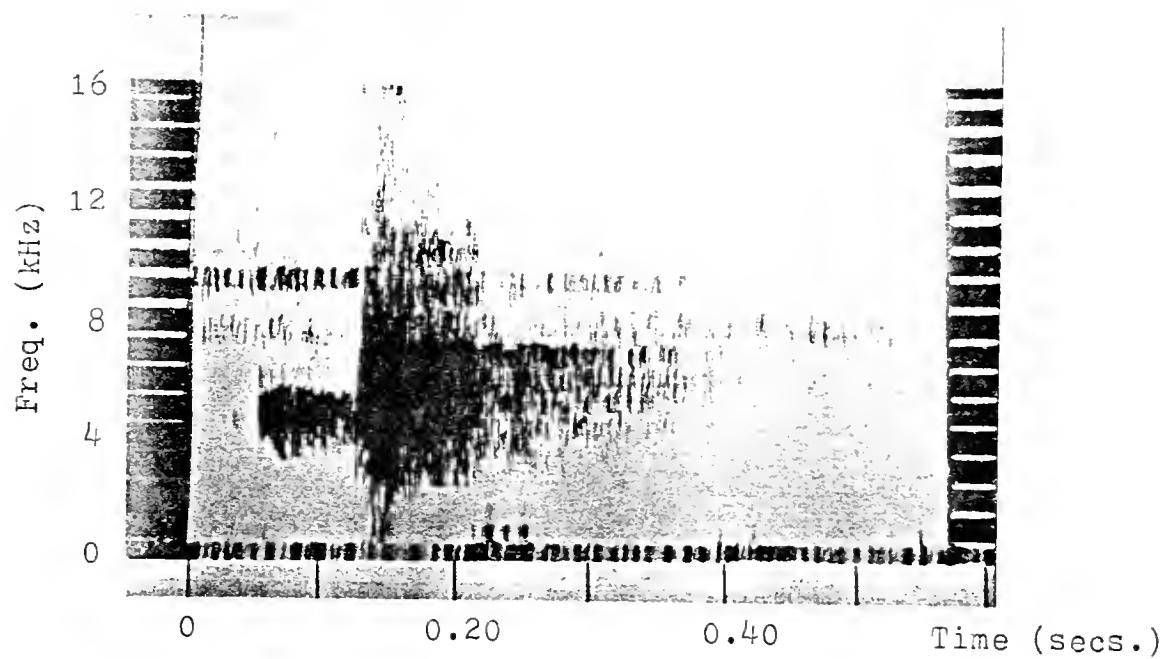


Figure 3. Two-Unit Chirp

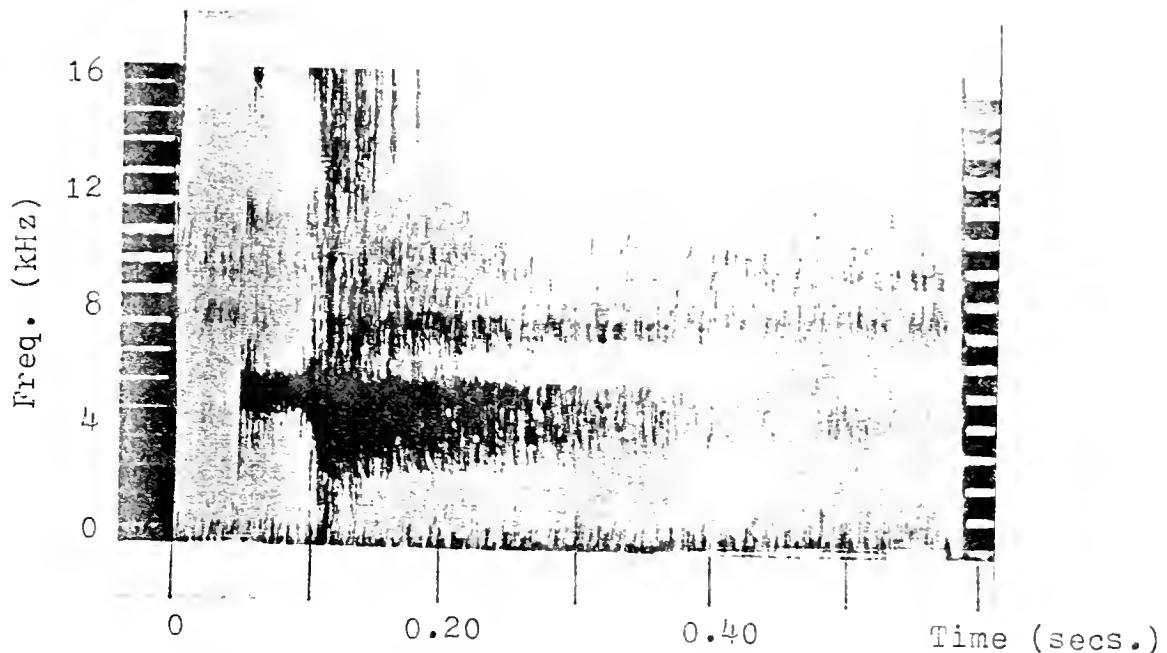


Figure 4. Two-Unit Chirp

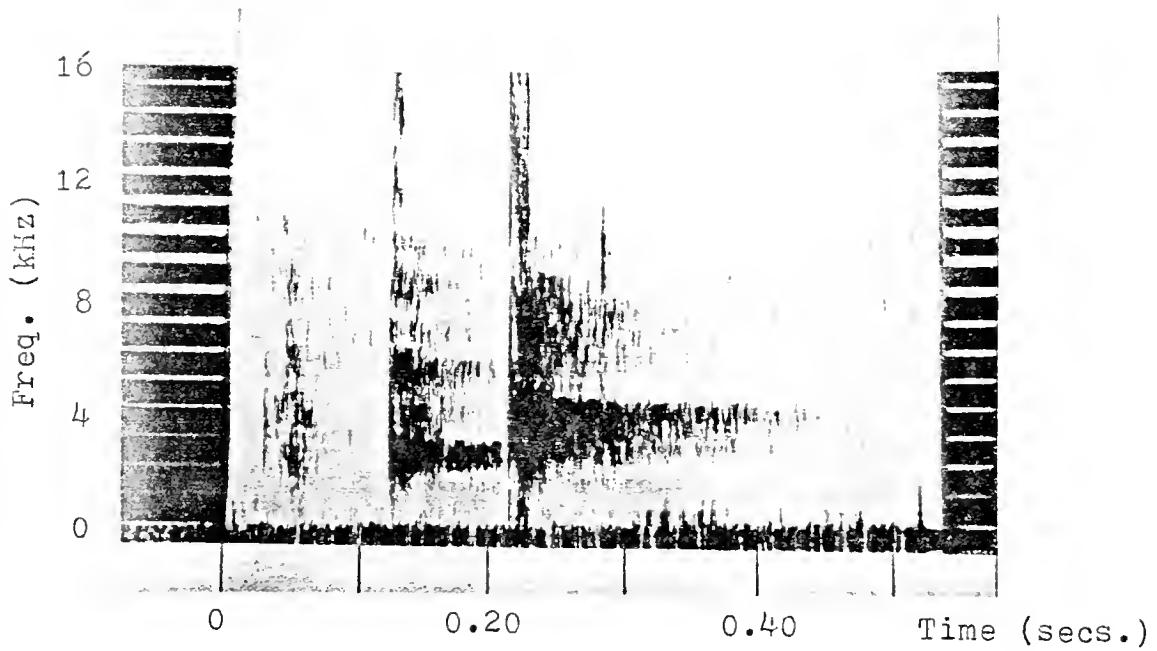


Figure 5. Three-Unit Chirp

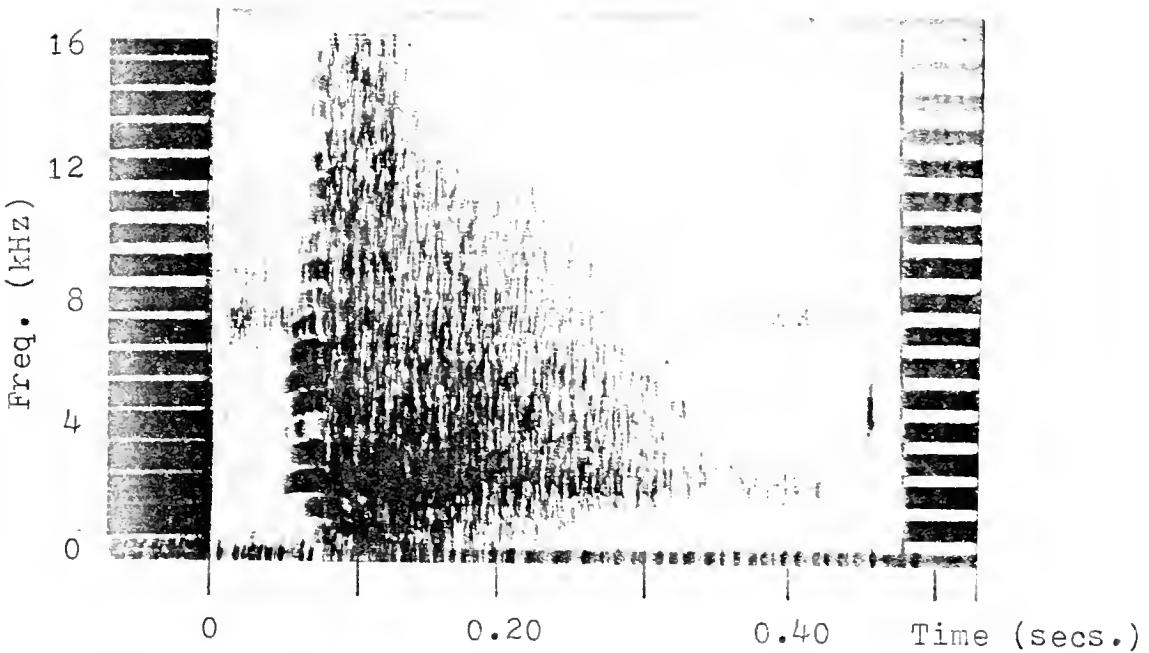


Figure 6. Nyah

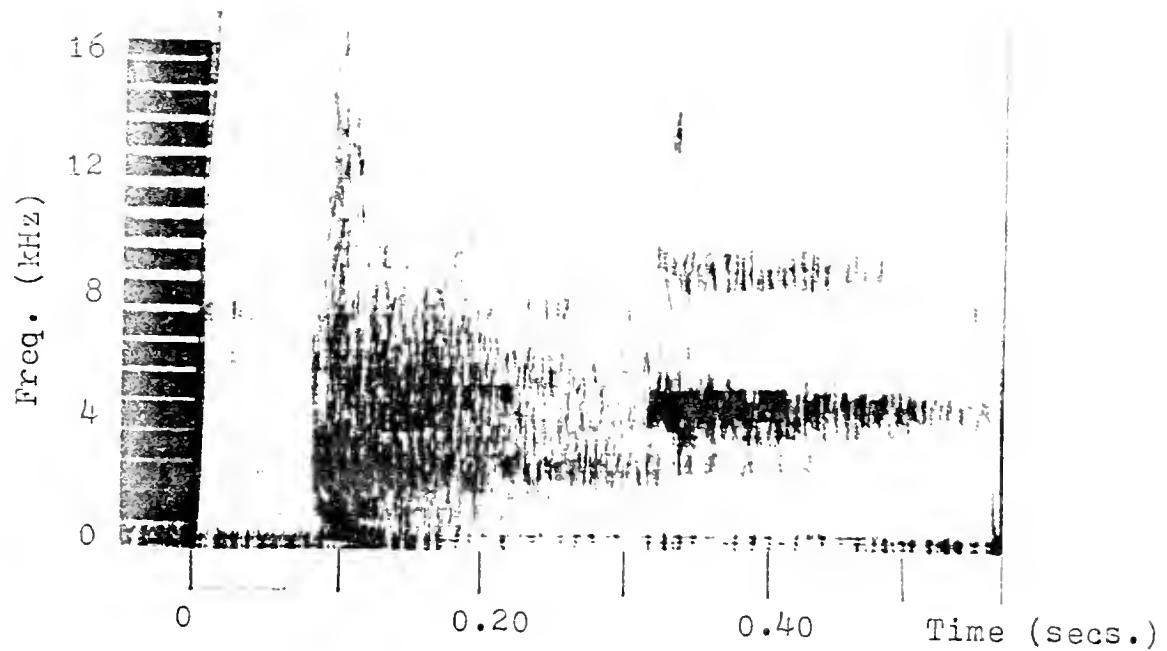


Figure 7. Short Nyah
(short nyah followed by chirp of another Sykes)

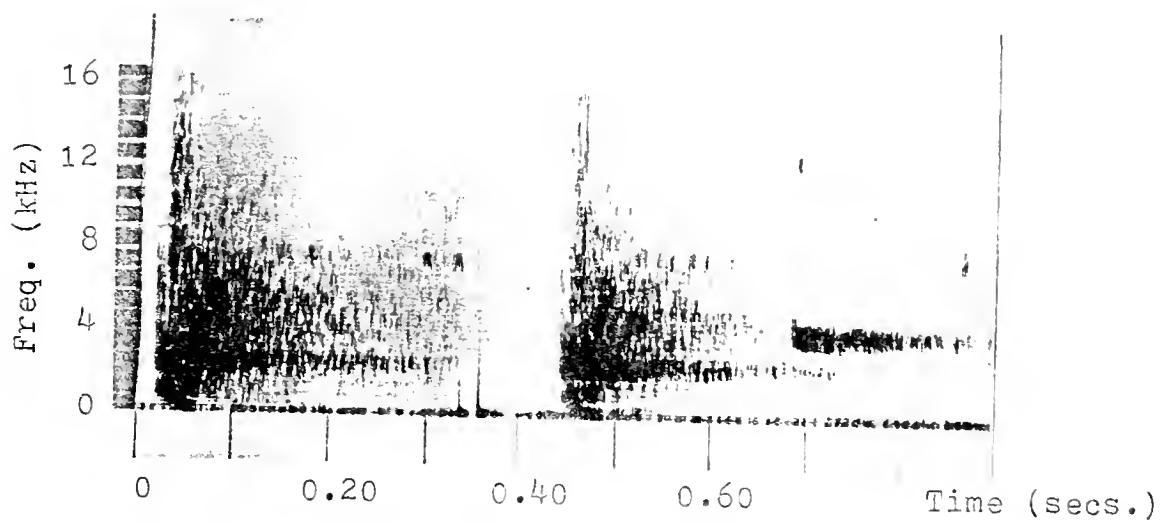


Figure 8. Short Nyah
(short nyahs followed by chirp of another Sykes)

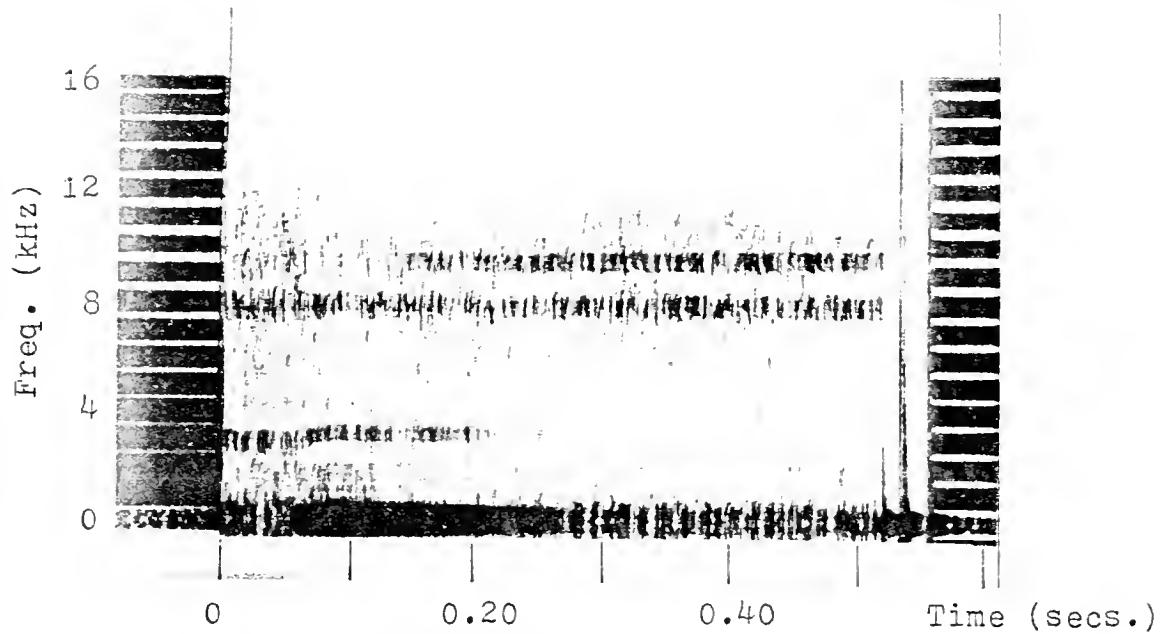


Figure 9. Boom
(ignore background noise at 3 kHz and 8-10 kHz)

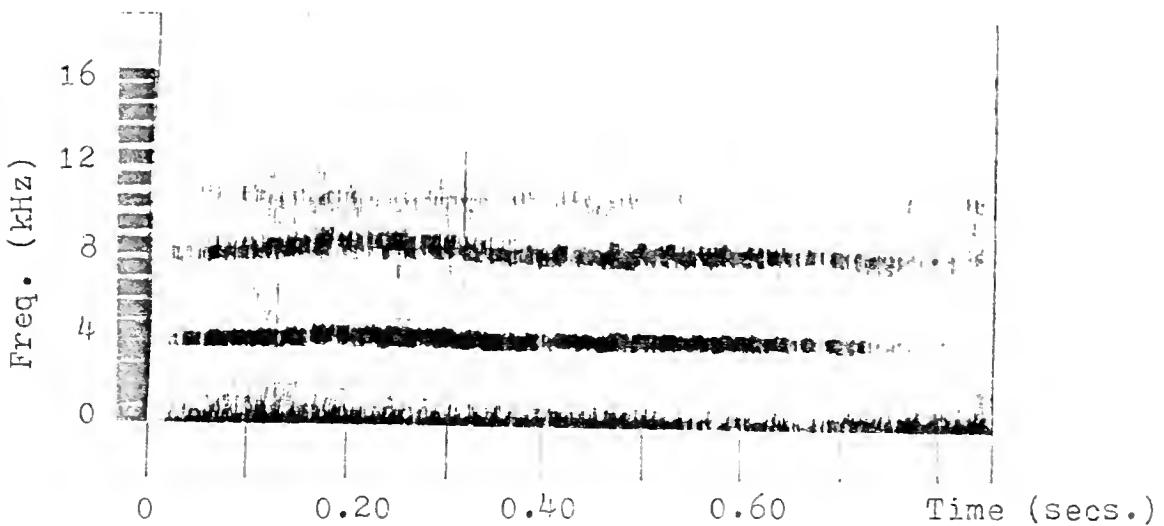


Figure 10. Squeal

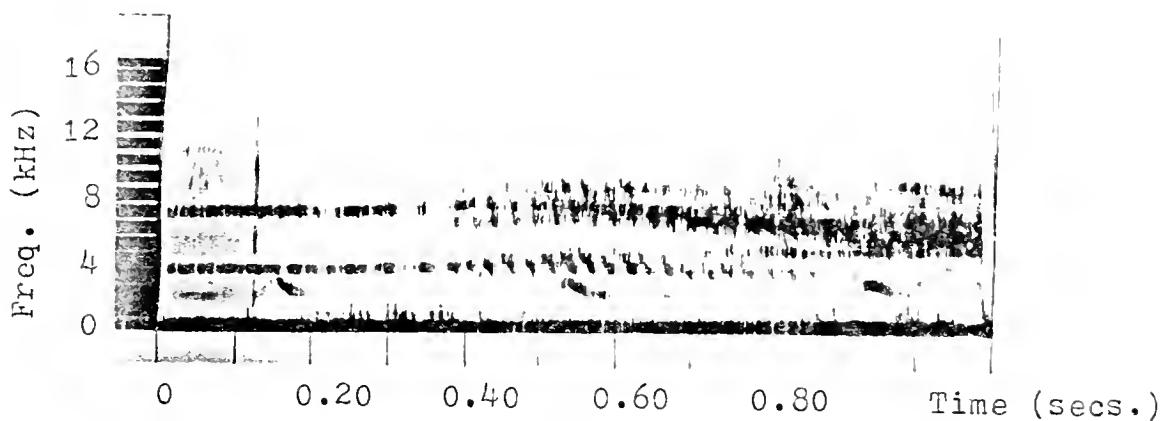


Figure 11. Shriek
(ignore background noise at 2-3 kHz)

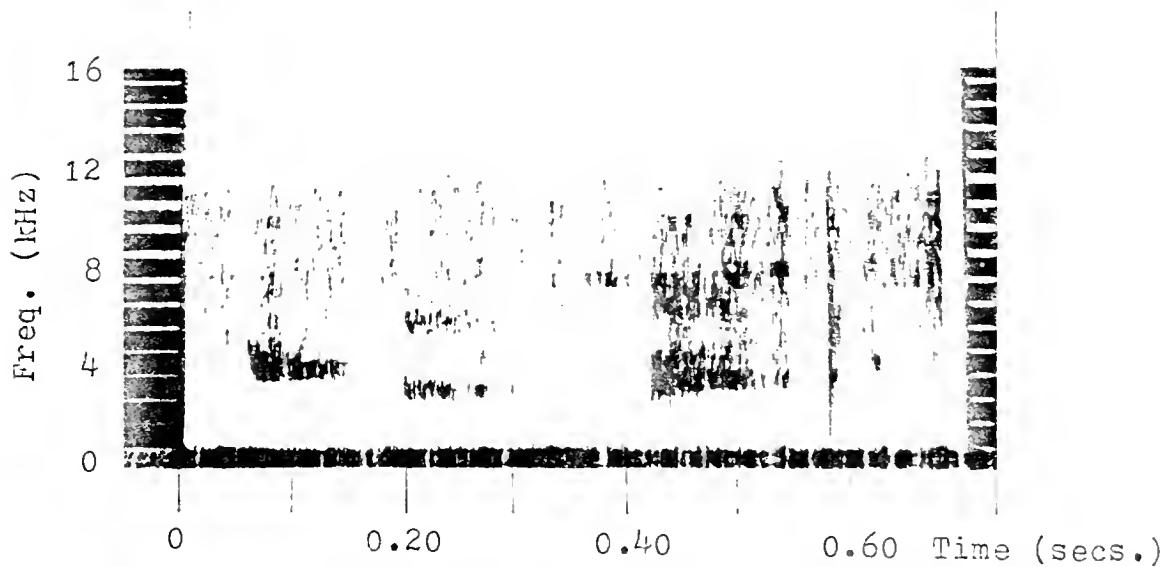


Figure 12. Chut

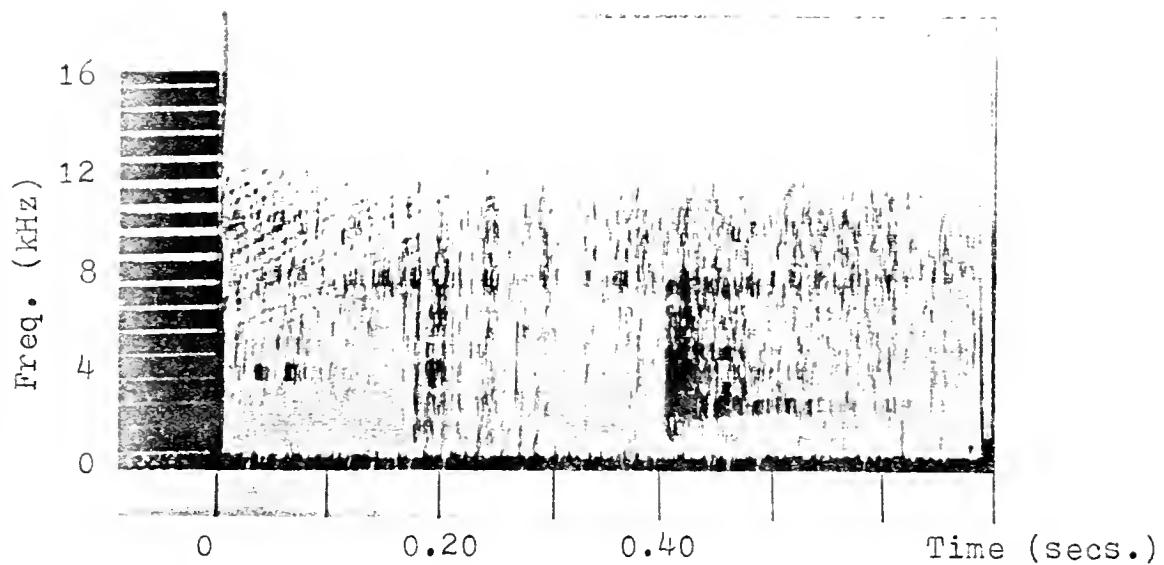


Figure 13. Chut
(ignore background noise at 7-8 kHz)

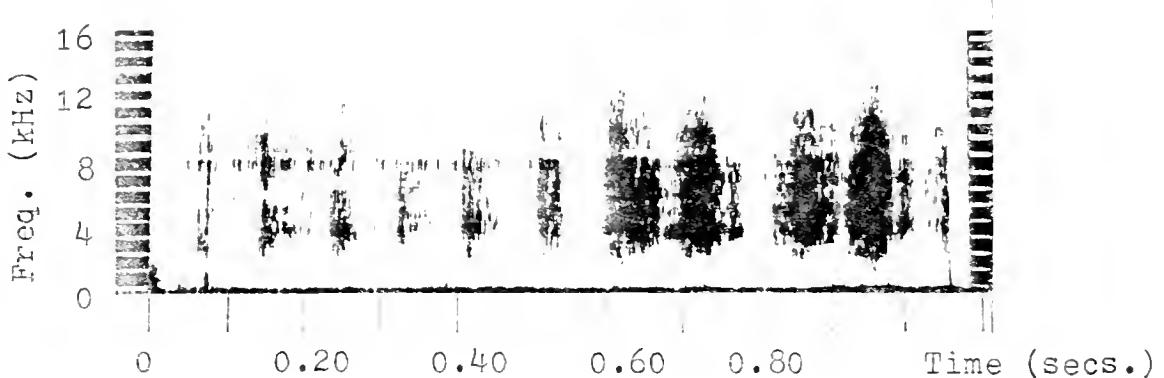


Figure 14. Chutter

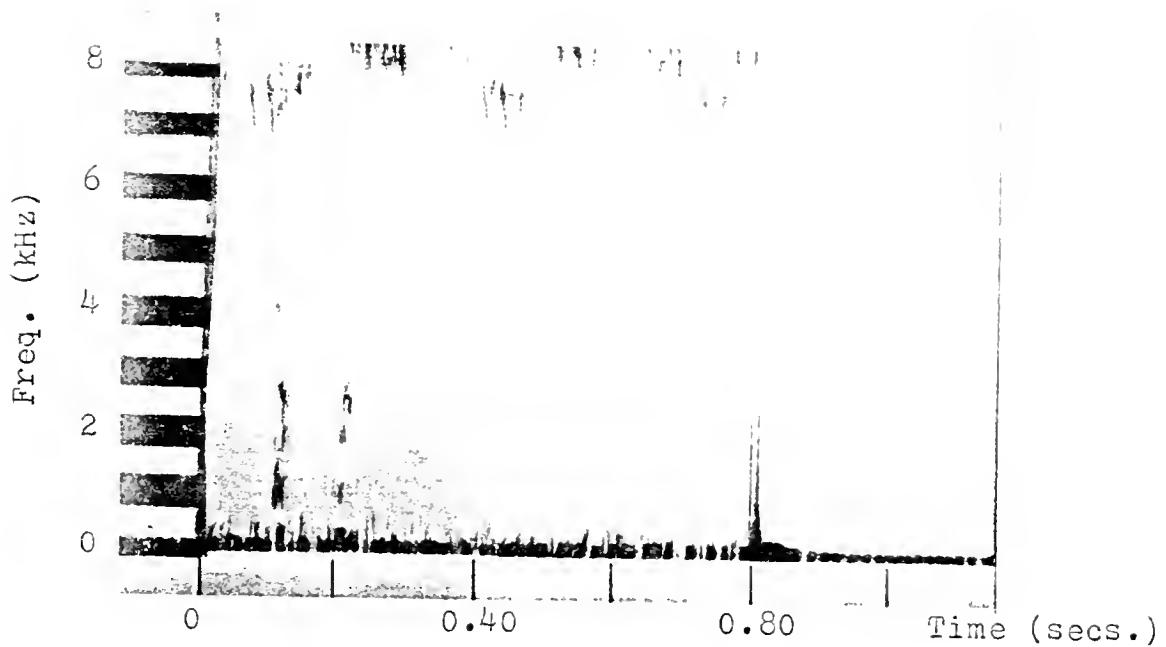


Figure 15. Low, Short Chutter
(ignore background noise at 7-8 kHz and at 0.80 secs.)

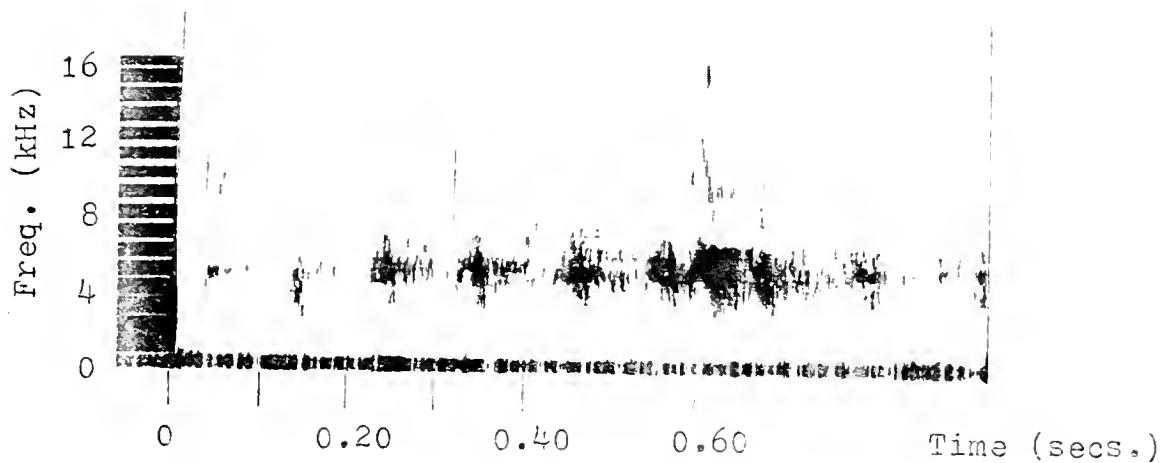


Figure 16. Chutter-Squeal
(chirp of another Sykes superimposed at 0.60 secs.)

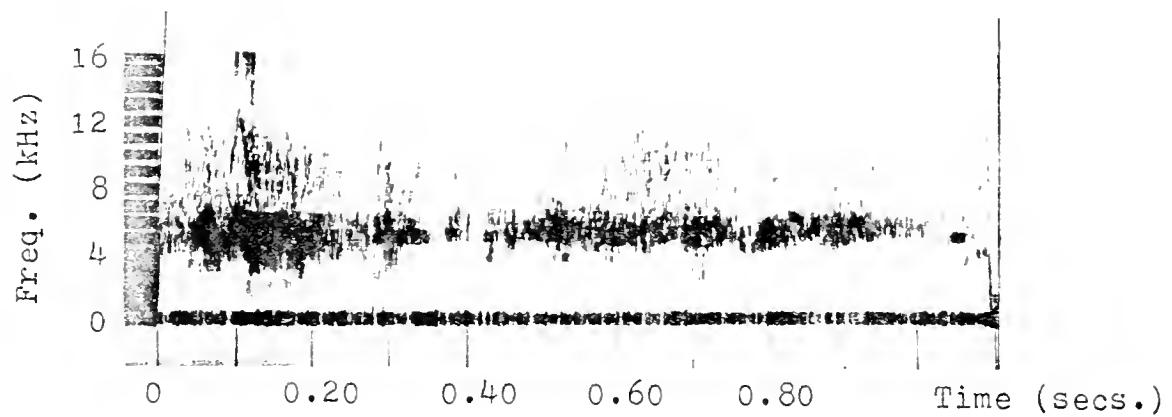


Figure 17. Chutter-Squeal (continued)
(chirp of Fig. 16 superimposed at 0.10 secs.)

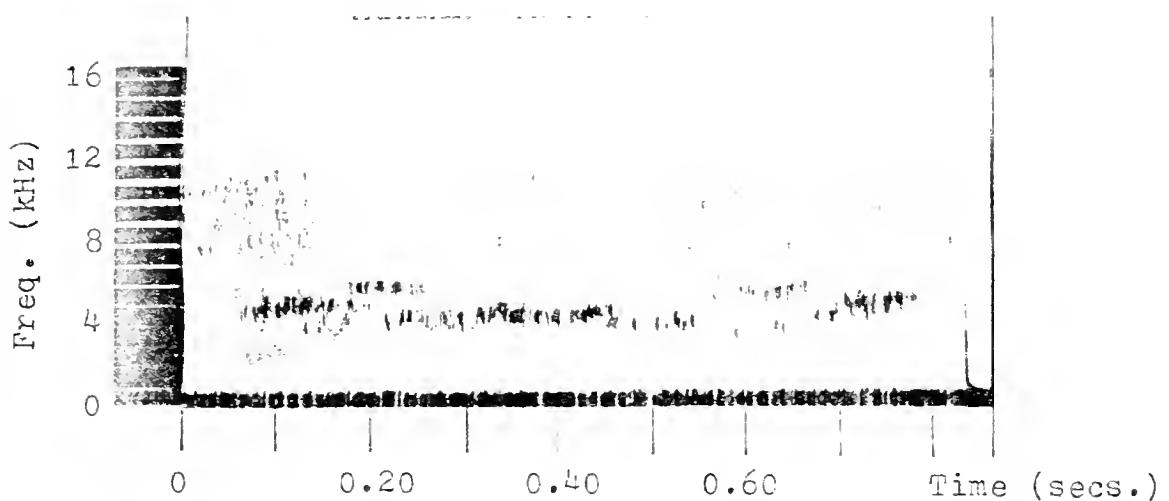


Figure 18. Chutter-Squeal (continued)

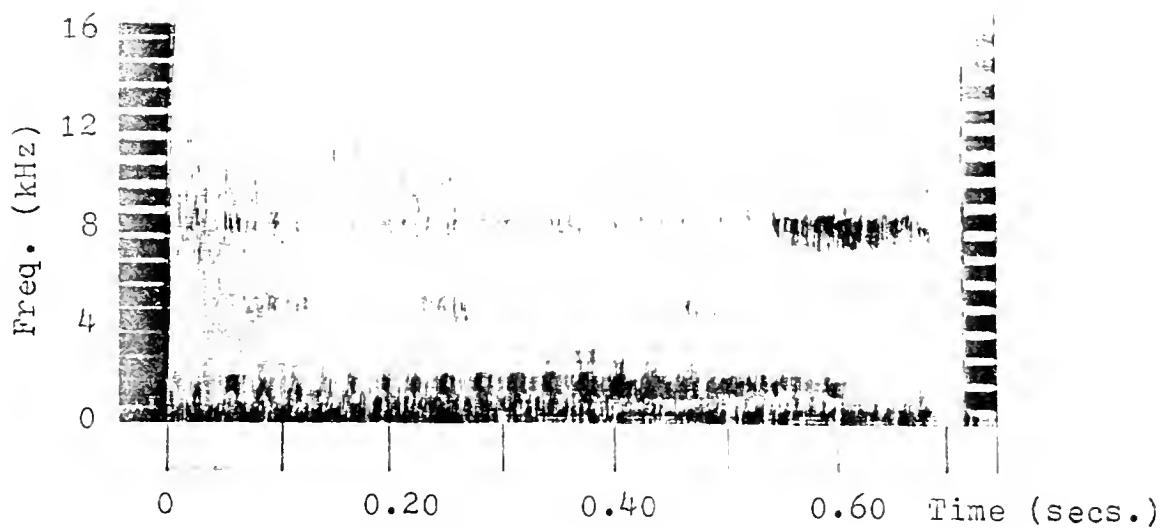


Figure 19. Growl
(ignore background noise at 7-8 kHz)

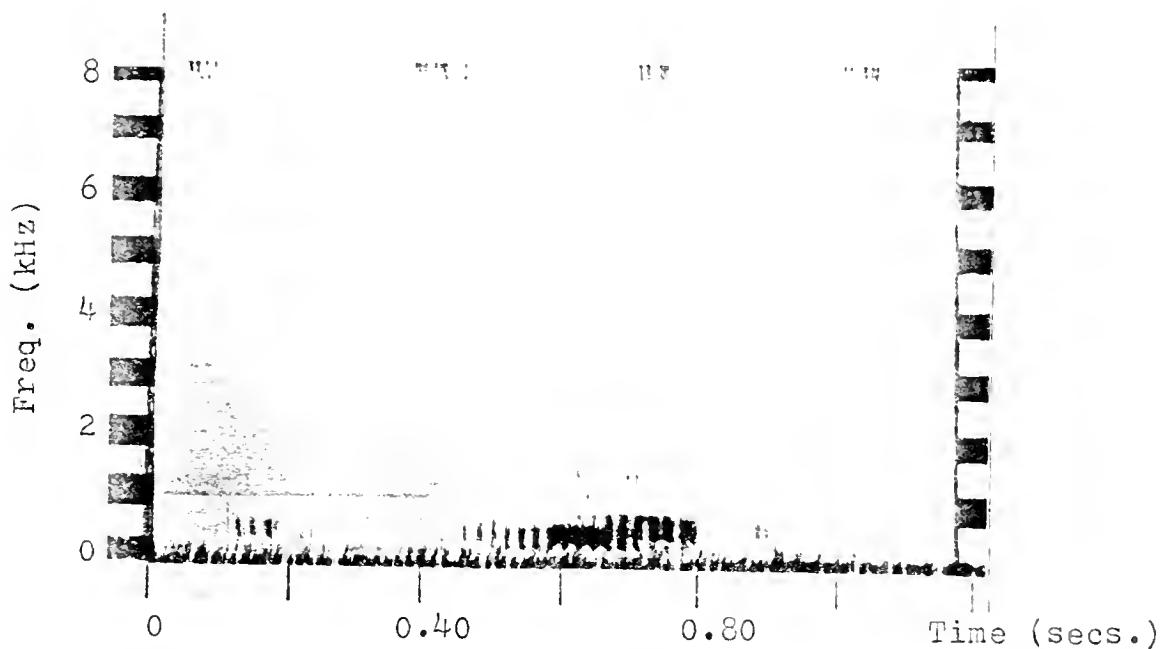


Figure 20. Growl
(ignore background noise at 7-8 kHz)

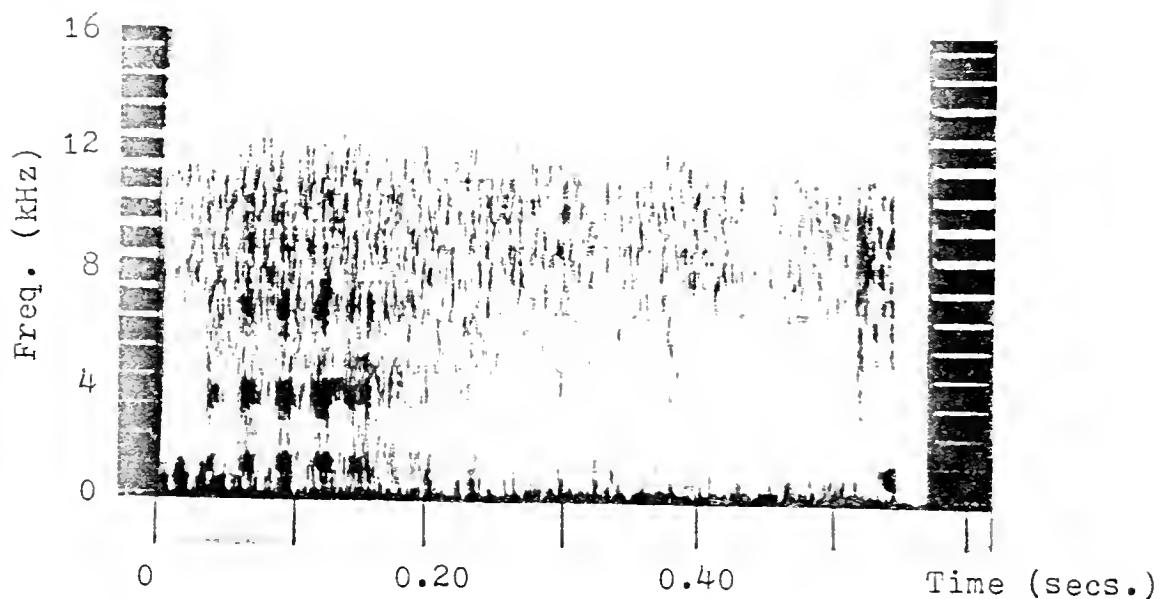


Figure 21. Err

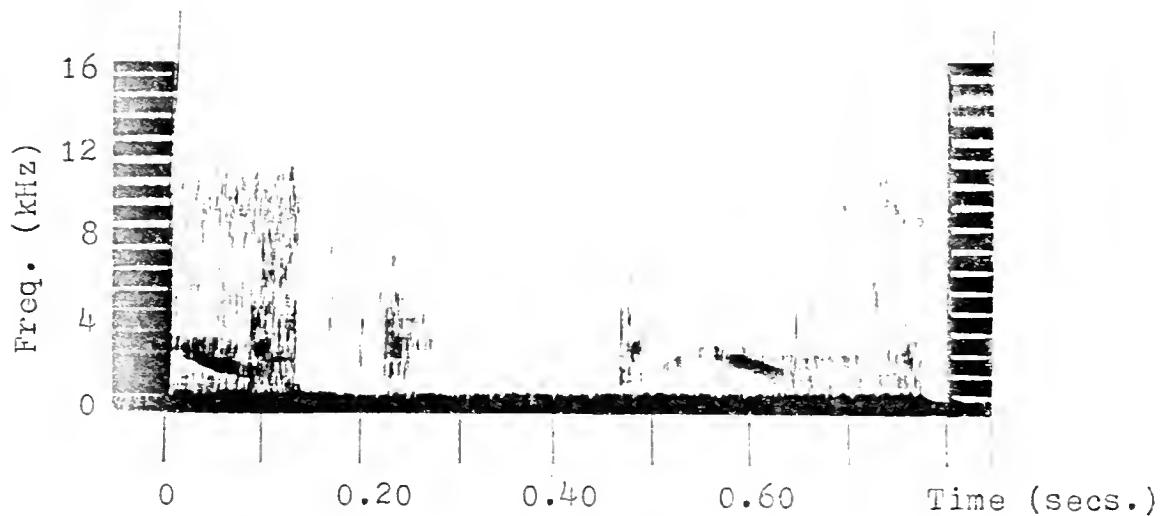


Figure 22. Uh

(ignore background noise at 0-0.07 secs. and 0.50-0.65 secs.)

COLOBUS MONKEY

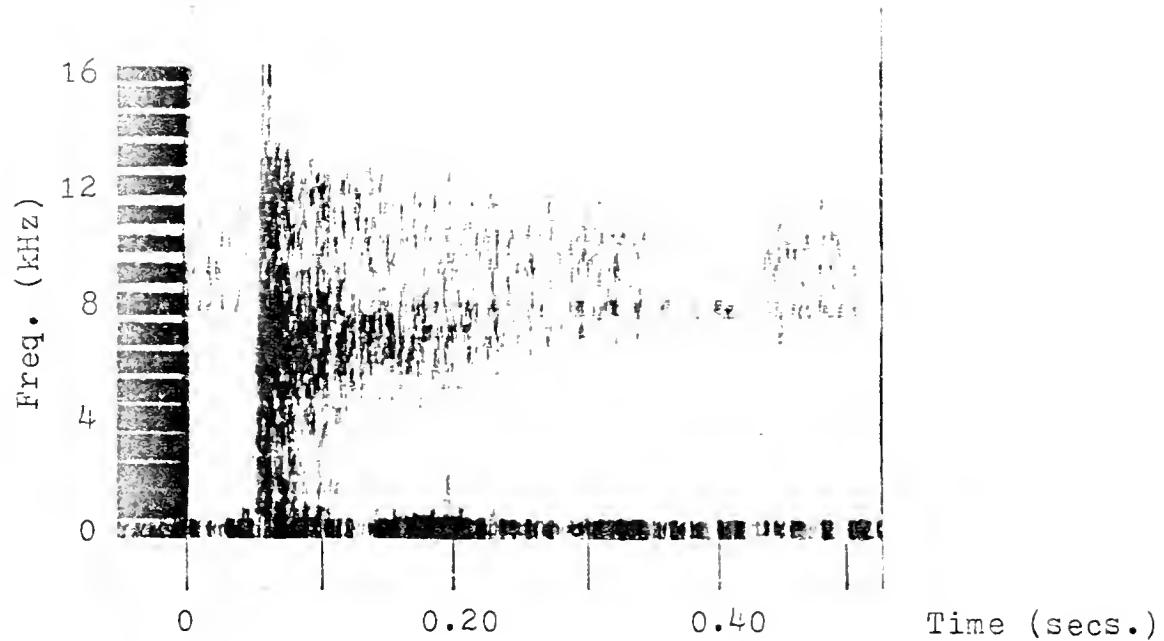


Figure 23. Snort

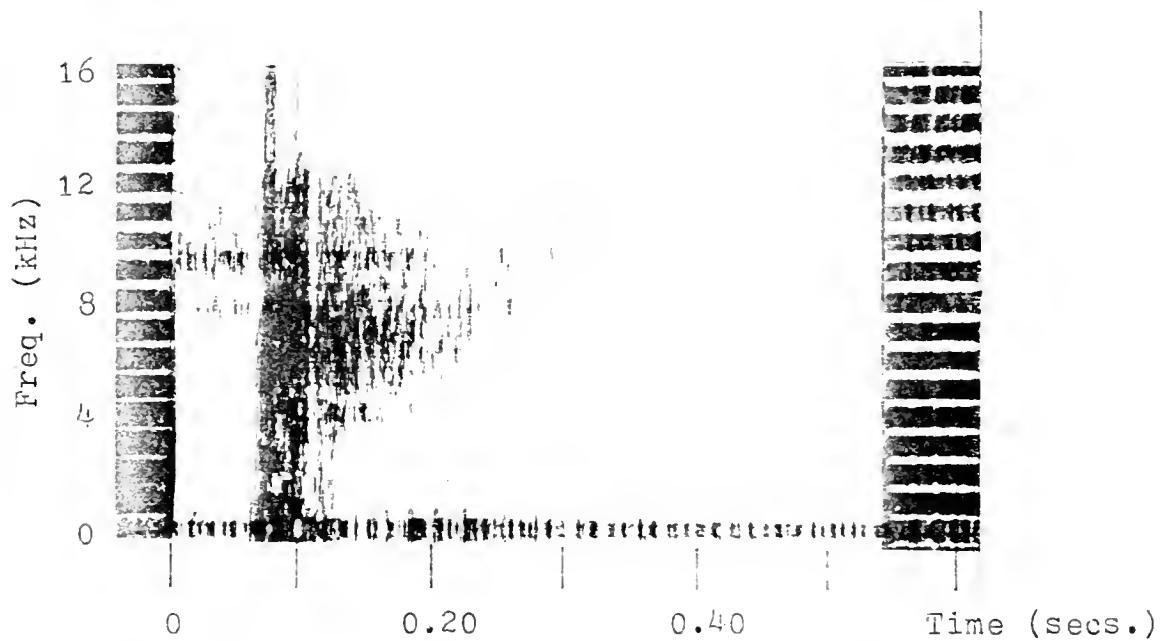


Figure 24. Snort

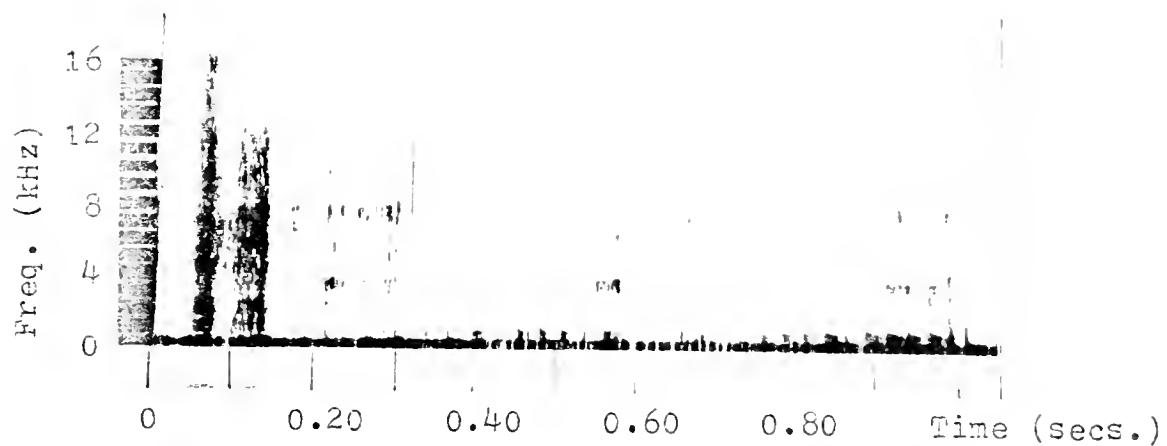


Figure 25. Snort-Croak

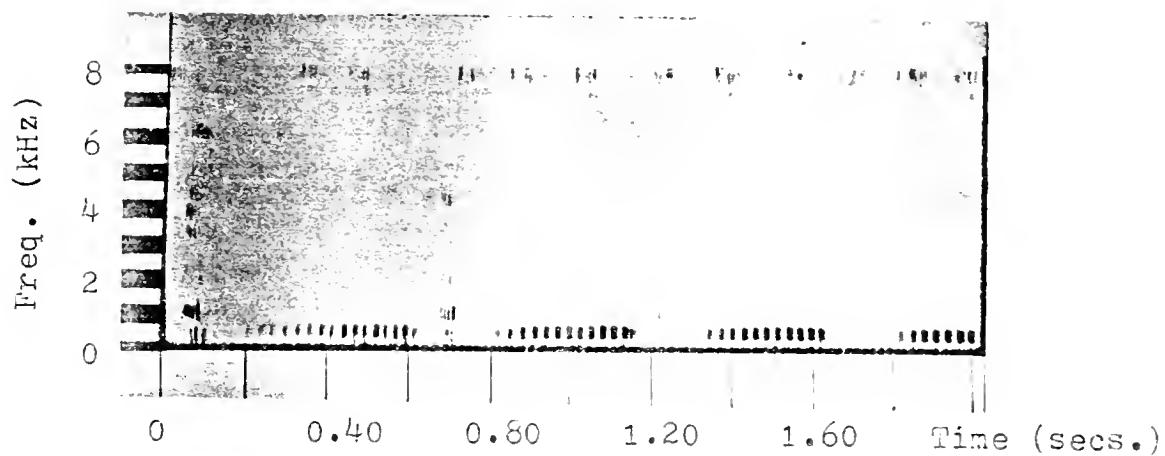


Figure 26. Snort-Croak
(ignore background noise at 8 kHz)

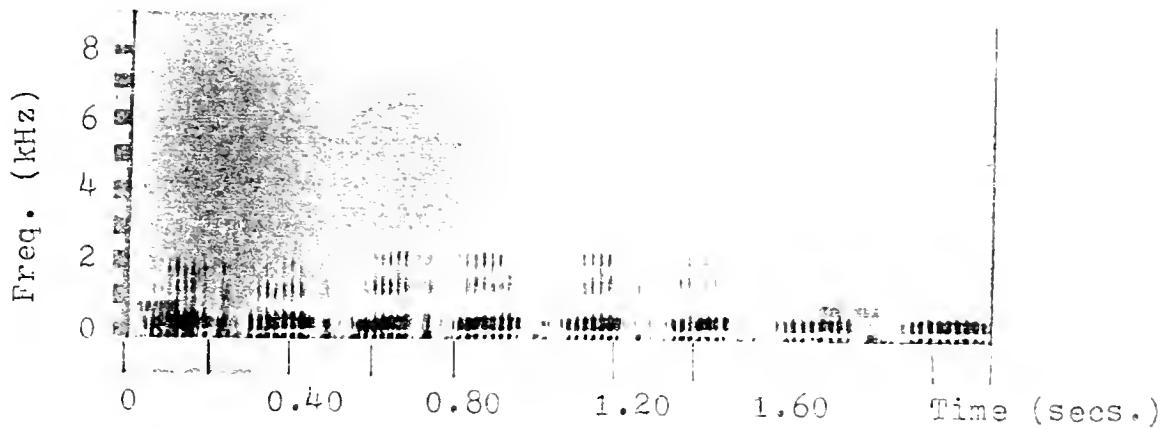


Figure 27. Snort-Croak

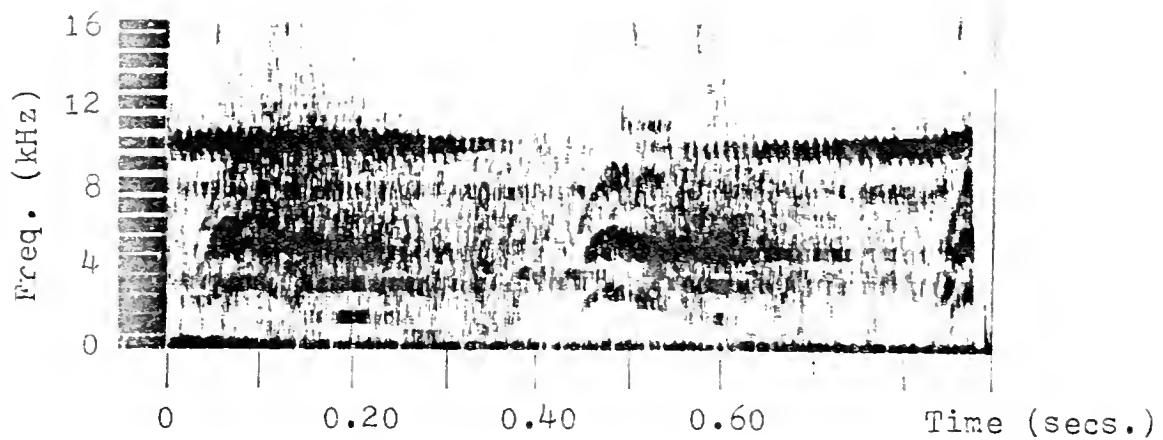


Figure 28. Gecker-White Infant
(ignore background noise at 10 kHz)

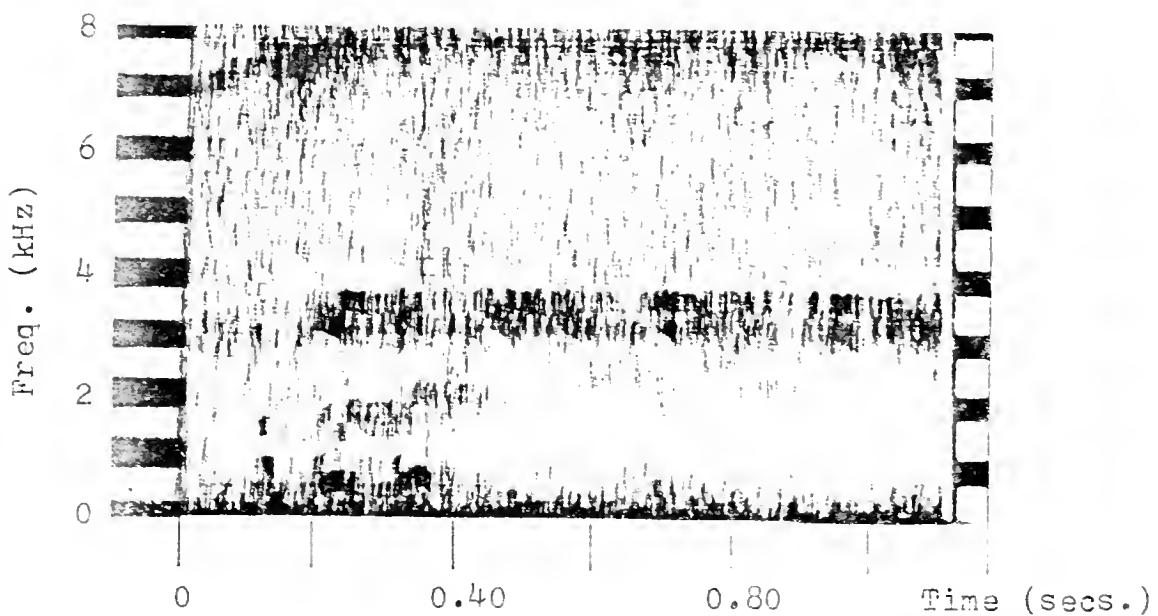


Figure 29. Err-White Infant
(ignore background noise at 3-4 kHz)

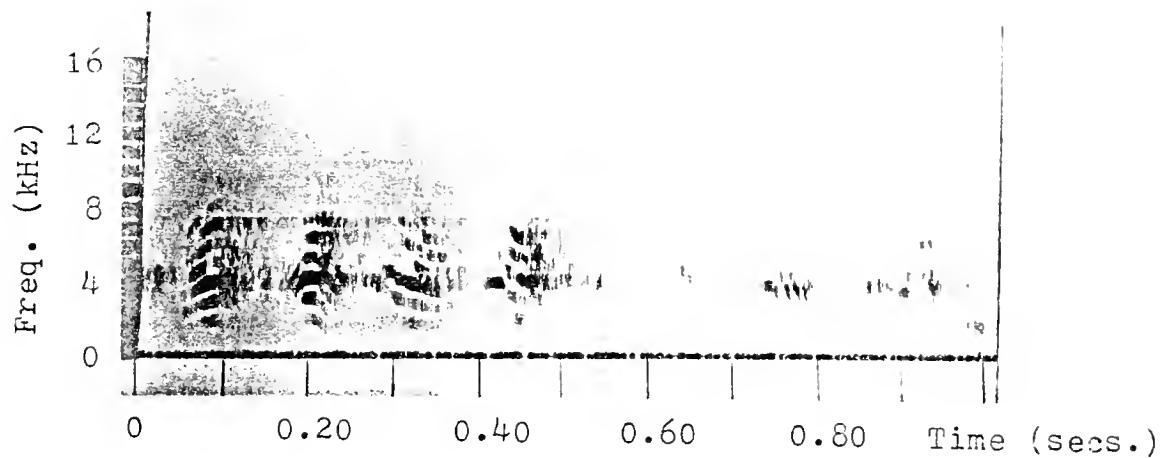


Figure 30. Gecker-Juvenile

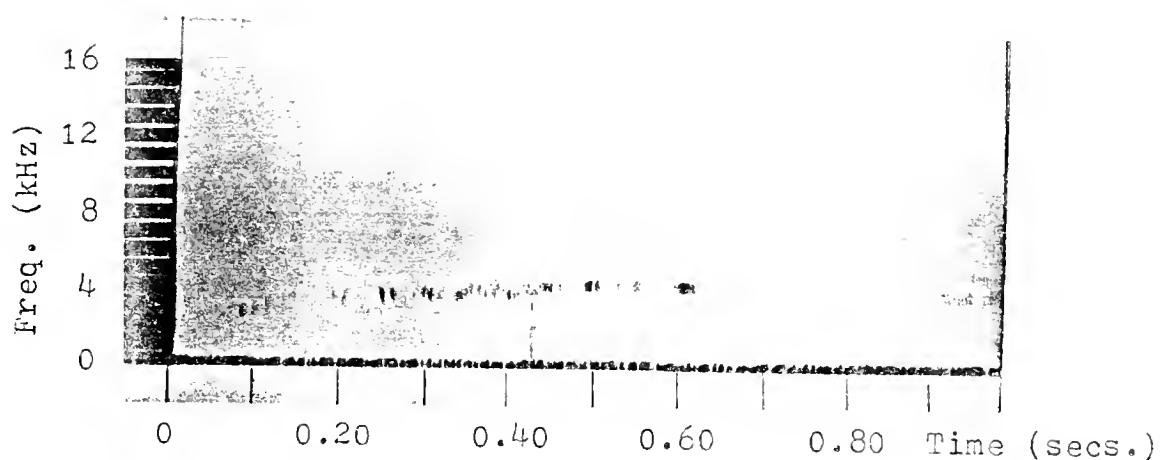


Figure 31. Gecker-Juvenile

BABOON

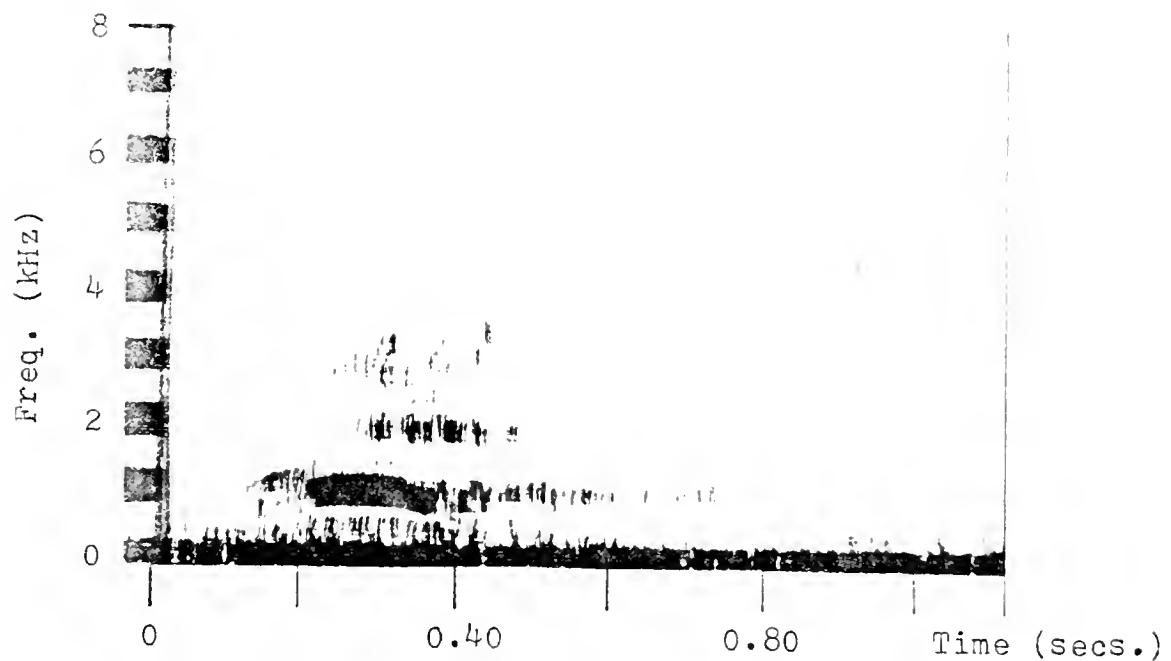


Figure 32. Two-Phase Bark

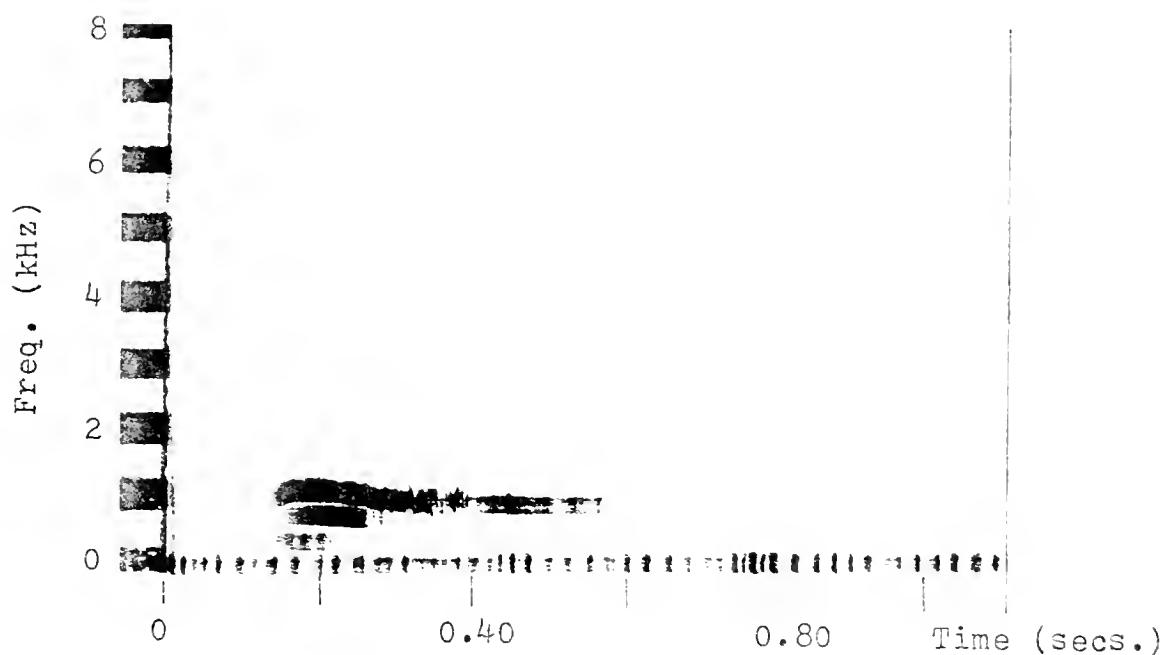


Figure 33. Two-Phase Bark

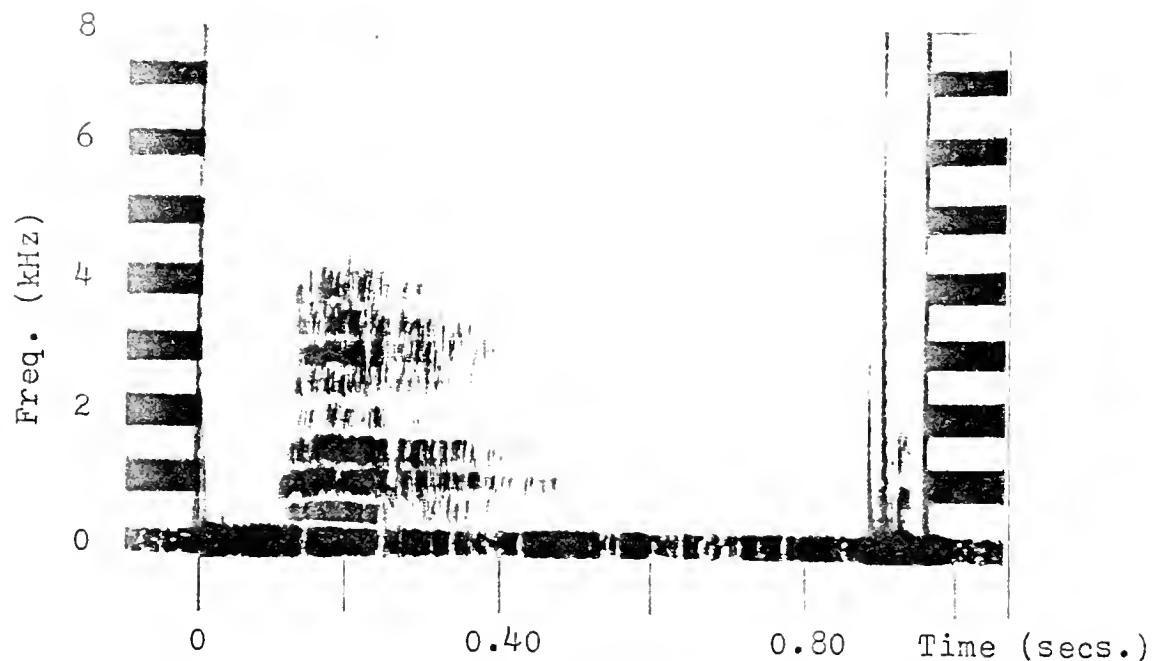


Figure 34. Bark I
(ignore background noise at 0.90 secs.)

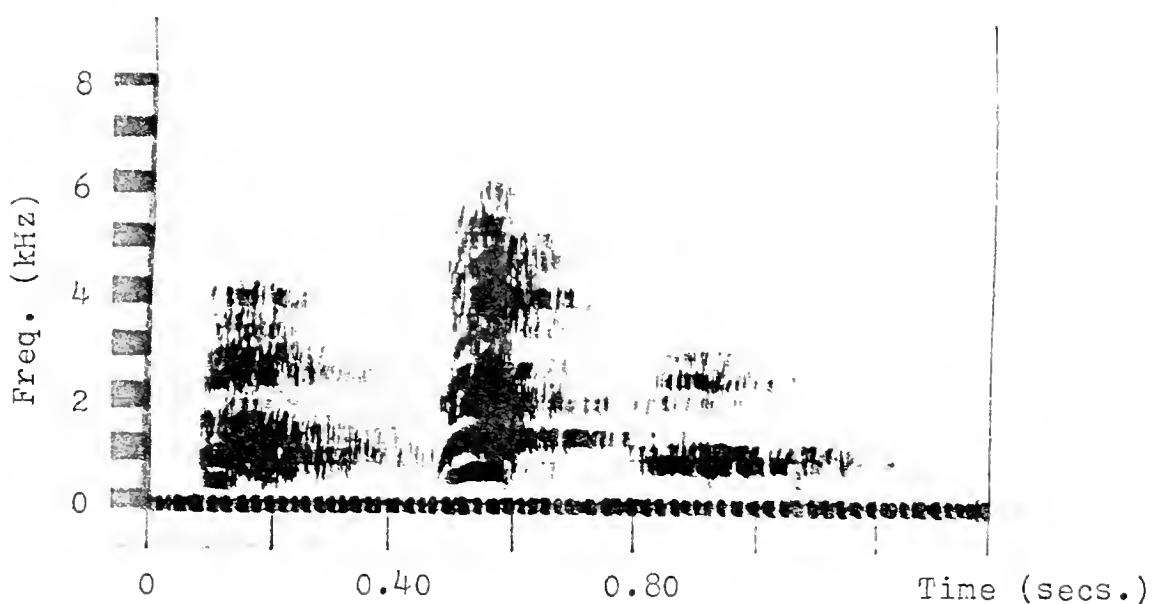


Figure 35. Bark I, Yak, Bark II

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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